Table 1

Loligo opalescens collected north of latitude 55° from 1982 through 1984.

| Collection number* | Collection data | | | |
|-------------------------|--|--------------|--|----------------------------------|
| | Samples | Date | Southeast Alaska location | Method, depth |
| | | Live | captures | |
| AB 82-20 | 335 egg capsules | 21 July 1982 | Rowan Bay, Kuiu Island 56°39.4'N, 134°15.5'W | Scuba diving, 12-15 m |
| AB 83-21 | 2 juveniles (57 & 87 mm ML)** | 4 Aug. 1983 | Port Conclusion, Baranof Island 56°15.8'N, 134°39.8'W | Trawl, 18–37 m on hard bottom |
| AB 84-54 NMML 454 | 230+ specimens (57-116 mm ML) (27 specimens are at AB, 63 at NMML; rest discarded) | 4 May 1984 | West of Myriad Islands 57°33.6'N, 136°22.3'W | Trawl, 126 m on hard bottom |
| AB 84-71 | 1 male (86 mm ML) | 17 July 1984 | Lisianski Inlet, east side Yakobi Island, 58°0.6'N, 136°28'W | Purse seine, 0-45 m |
| AB 84-72 | 1 juvenile (57 mm ML) | 18 July 1984 | Herbert Graves Island 57°41'N, 136°11'W | Purse seine, 0–45 m |
| | | Stoma | ch contents | |
| AB 83-47 | 2 juveniles (21 & 22 mm ML) | 10 Apr. 1982 | Whale Bay, Baranof Island 56°36.3'N, 135°2.5'W | Chinook salmon stom- ach |
| AB 83-48 | 1 adult (89 mm ML) | 14 Apr. 1982 | Whale Bay, Baranof Island 56°36.3'N, 135°2.5'W | Chinook salmon stom- ach |
| AB 83-49 | 1 adult (93 mm ML) | 18 Aug. 1982 | Surge Bay, Yakobi Island 57°59.7'N, 136°33.1'W | Coho salmon stomach |
| AB 83-50 | 1 adult (81 mm ML) | 1 July 1983 | Hoktaheen, Yakobi Island 58°4.4'N, 136°33.0'W | Chinook salmon stom- ach |

^{*} Collections held at the Auke Bay Laboratory, Auke Bay, Alaska (AB) or the National Marine Mammal Laboratory, Seattle, Washington (NMML).

** ML = dorsal mantle length.

(FIELDS, 1965). Frequency of spawning in southern Southeast Alaska is unknown.

The two periods during which Loligo opalescens has been documented in Southeast Alaska are associated with warmer than average waters: REID (1961) reported squids, including L. opalescens, as common in stomach contents (1.3-13.8%) of troll-caught chinook salmon during the strong 1957-1958 El Niño, and STREET (1983) collected L. opalescens in southern Southeast Alaska from 1980 to 1982 following a warming trend that began in 1970 (ROYER, 1985). The presence of L. opalescens as far north as Cross Sound in northern Southeast Alaska during 1983 and 1984 probably resulted from a combination of the 1982-1983 El Niño and the long-term warming trend. The possibility that this warming trend resulted in an overall increase in abundance of L. opalescens is consistent with observations in central California where successive warm years resulted in increased harvest (McInnis & Broenkow, 1979). Increased landings in Washington also occur during or following a strong El Niño (SHOENER & FLUHARTY, 1985). During the 1982-1983 El Niño, squid from the more southerly areas may have established small spawning populations along the coast from southern Baranof Island to Cross Sound. Although the specimens collected in 1984 from the Myriad Islands were in spawning condition, no specimens of *L. opalescens* have been collected during subsequent zooplankton and demersal fish surveys in the same general area. It appears, therefore, that permanent populations were not established.

Table 2
Sex, maturity, and size of Loligo opalescens collected west of the Myriad Islands, Southeast Alaska, 4 May 1984.
Measurements made before preservation.

| Sex and maturity | Mean dorsal mantle length (mm) | Number measured $(n = 202)$ | |
|---------------------|-----------------------------------|-----------------------------|--|
| Females | 83.7 | 109 | |
| Mature | 84.4 | 102 | |
| Immature | 73.7 | 7 | |
| Males | 78.4 | 93 | |
| Mature | 82.0 | 57 | |
| Immature | 72.6 | 36 | |

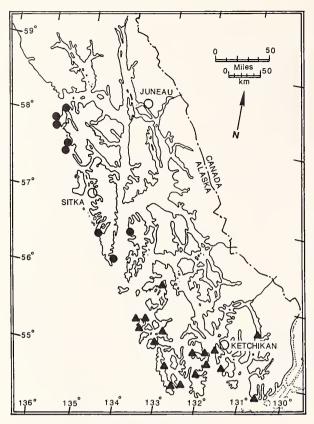


Figure 1

Capture localities of *Loligo opalescens* (closed circles) in northern Southeast Alaska and localities of observations (triangles) reported by STREET (1983) in southern Southeast Alaska.

ACKNOWLEDGMENTS

We thank Mr. Clifford Fiscus, Dr. Katharine Jefferts, and Ms. Sara Maupin for confirming the identification of the specimens from the Myriad Islands and for sorting and storing them at the National Marine Mammal Laboratory. We thank Mr. Richard Haight for release of the sample and data.

LITERATURE CITED

Bernard, F. R. 1970. A distributional checklist of the marine molluscs of British Columbia: based on faunistic surveys since 1950. Syesis 3:75-94.

BERNARD, F. R. 1980. Preliminary report on the potential

commercial squid of British Columbia. Can. Tech. Rept. Fish. Aquat. Sci. No. 942. 51 pp.

FIELDS, W. G. 1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Calif. Dept. Fish Game Fish Bull. 131:1–108.

HIXON, R. F. 1983. Loligo opalescens. Pp. 95-114. In: P. R. Boyle (ed.), Cephalopod life cycles. Vol. 1. Species accounts. Academic Press: New York.

JONES, J. D. 1978. Southeastern Alaska sea surface temperatures, 1964–1974. U.S. Dept. Commerce, NOAA, NMFS/ NWAFC Proc. Rept. 2725 Montlake Blvd., Seattle, Washington 98112. 67 pp.

KARINEN, J. F., B. L. WING & R. R. STRATY. 1985. Records and sightings of fish and invertebrates in the eastern Gulf of Alaska and oceanic phenomena related to the 1983 El Niño event. Pp. 253–267. *In:* W. S. Wooster & D. L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean. Wash. Sea Grant Prg. University of Washington, Seattle, Washington.

McInnis, R. R. & W. W. Broenkow. 1979. Correlations between squid catches and oceanographic conditions in Monterey Bay, California. Pp. 161–170. *In:* W. W. Recksiek & H. W. Frey (eds.), Biological, oceanographic, and acoustic aspects of the market squid *Loligo opalescens* Berry. Calif. Dept. Fish Game Fish Bull. 169.

REID, G. M. 1961. Stomach content analyses of troll-caught salmon in southeastern Alaska, 1957–58. U.S. Fish Wildl. Serv. SSR-F 379. 8 pp.

ROPER, C. F. E., M. J. SWEENEY & C. E. NAUEN. 1984. FAO species catalogue. Vol. 3. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Fish. Synop. (125) Vol. 3. 227 pp.

ROYER, T. C. 1985. Coastal temperature and salinity anomalies in the northern Gulf of Alaska. Pp. 107-115. *In:* W. S. Wooster & D. L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean. Wash. Sea Grant Prg. University of Washington, Seattle, Washington.

SHIMEK, R. L., D. FYFE, L. RAMSEY, A. BERGEY, J. ELLIOT & S. GUY. 1984. A note on spawning of the Pacific market squid, *Loligo opalescens* (Berry, 1911), in the Barkley Sound region, Vancouver Island, Canada. Fish. Bull., U.S. 82(2): 445–446.

SHOENER, A. & D. L. FLUHARTY. 1985. Biological anomalies off Washington in 1982–83 and other major Niño periods. Pp. 211–225. *In:* W. S. Wooster & D. L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean. Wash. Sea Grant. Prg. University of Washington, Seattle, Washington.

STREET, D. 1983. Squid fishery development project of Southeast Alaska. Report prepared for Alaska Fisheries Development Foundation, Inc., Anchorage, Alaska. 60 pp.

WILLIAMSON, R. S. 1965. Southeastern Alaska sea surface temperatures, 1959–1963. U.S. Fish Wildl. Serv., Data Rept. 8. 41 pp.

WING, B. L. 1985. Salmon stomach contents from the Alaska troll logbook program, 1977–1984. U.S. Dept. Commerce, NOAA, Tech. Memo. NMFS F/NWC-91. 43 pp.

A Review of the Recent Eastern Pacific Acanthochitoninae (Mollusca: Polyplacophora: Cryptoplacidae) with the Description of a New Genus, Americhiton

by

G. THOMAS WATTERS

The Museum of Zoology, The Ohio State University, Columbus, Ohio 43210, USA

Abstract. Recent species of the Acanthochitoninae in the eastern Pacific are reviewed. Members of the genus Acanthochitona include: A. angelica Dall, 1919, A. avicula (Carpenter, 1864), A. exquisita (Pilsbry, 1893), A. ferreirai Lyons, 1988, A. hirudiniformis hirudiniformis (Sowerby I, 1832), A. hirudiniformis peruviana (Leloup, 1941), and A. imperatrix Watters, 1981. A new genus, Americhiton, is created for A. arragonites (Carpenter, 1857), type species, and the western Atlantic species A. andersoni (Watters, 1981), A. balesae (Abbott, 1954), and A. zebra (Lyons, 1988).

INTRODUCTION

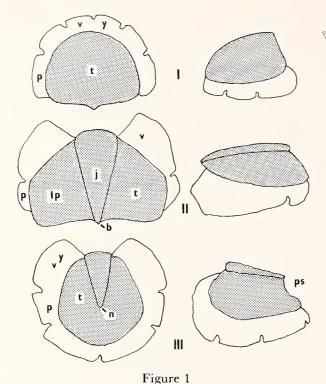
The family Cryptoplacidae, containing the two subfamilies Cryptoplacinae and Acanthochitoninae, includes diverse, predominantly tropical and subtropical chitons that have a confusing taxonomic history. Although this group is a significant component of most chiton faunas, the identification of even the most common species may be problematical. In recent years several attempts have been made to clarify the status of New World chitons including cryptoplacids. THORPE (1971) published an account of the eastern Pacific species and KAAS (1972) followed with Caribbean taxa. In 1980, I completed an unpublished Master's Thesis review of the family Cryptoplacidae in the New World utilizing scanning electron microscopy (SEM); my brief 1981 articles were extracted from that thesis. Ferreira (1985) published a study of the chitons of Barbados in which he reached several incongruous and unfortunate conclusions on the family Cryptoplacidae. Lyons (1988a) also reviewed the Caribbean species of this family using SEM, and described six new species (one, however, was from the eastern Pacific), and corrected much of the confusion instituted by Ferreira. This report, modified from my 1980 thesis, covers the remaining eastern Pacific species.

The results of this study indicate that eight species and subspecies of Cryptoplacidae occur in the Recent of the eastern Pacific. All belong to the subfamily Acanthochi-

toninae (the Caribbean *Choneplax lata* (Guilding, 1829) is the only New World member of the Cryptoplacinae). The eastern Pacific taxa are as follows:

Acanthochitona angelica Dall, 1919
Acanthochitona avicula (Carpenter, 1864)
Acanthochitona exquisita (Pilsbry, 1893)
Acanthochitona ferreirai Lyons, 1988
Acanthochitona hirudiniformis hirudiniformis (Sowerby I, 1832)
Acanthochitona hirudiniformis peruviana (Leloup, 1941)
Acanthochitona imperatrix Watters, 1981
Americhiton arragonites (Carpenter, 1857), gen. nov.

In strict accordance with ICZN rules (Art. 50 (a)), I have cited Pilsbry or Dall as the author of Carpenter's manuscript names where appropriate. Although this manuscript was the basis of much of their work on chitons, and its influence duly noted by subsequent workers, it was never published by Carpenter. Nevertheless, both authors gave credit to Carpenter for names and descriptions of taxa, and under ICZN Art. 50 (a), Carpenter could be considered the "some other person . . . alone responsible both for the name and for satisfying the criteria of availability other than publication," and as such "then that person is the author of the name." Numerous workers have not resolved this problem to their satisfaction and have cited these species as "Carpenter in Dall" or "Car-



Shell plate morphology of *Acanthochitona*. I, anterior valve; II, intermediate valve; III, posterior valve; t, tegmentum; v, articu-

intermediate valve; III, posterior valve; t, tegmentum; v, articulamentum; lp, latero-pleural areas; j, jugum; b, beak; n, mucro; y, apophyses; p, insertion plates; ps, post-mucronal slope.

penter in Pilsbry." However, I feel that Dall and Pilsbry contributed enough to the description and illustration of Carpenter's species to warrant authorship, and Carpenter is not considered the author for these names in this review.

MATERIALS AND METHODS

SEM studies were conducted at the University of Rhode Island during 1976–1980 under the guidance of Dr. R. C. Bullock, who, along with E. Leloup, first emphasized the taxonomic importance of tegmental microstructure. All specimens were sonically cleaned, desiccated, and coated with gold-palladium prior to observation. Details of the procedure used to examine these specimens may be found in Bullock (1988).

ABBREVIATIONS USED IN TEXT

AJF—Private collection, now housed at CASIZ, of the late A. J. Ferreira; AMNH—American Museum of Natural History, New York; ANSP—Academy of Natural Science, Philadelphia; BMNH—British Museum (Natural History), London; CASIZ—California Academy of Sciences, San Francisco; DMNH—Delaware Museum of Natural History, Greenville; GTW—Private collection of G. T. Watters, Ohio State University; MCZ—Museum of Comparative Zoology, Cambridge; LACM—Natural

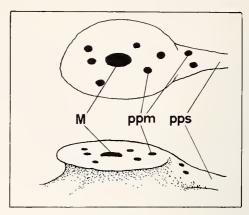


Figure 2

Hypothetical pustule morphology. M, macresthete; ppm, premacresthete micresthetes; pps, prepustular slope. The growing edge is to the left.

History Museum of Los Angeles County Museum; OSUM—Museum of Zoology, Ohio State University; RCB—Private collection of R. C. Bullock, University of Rhode Island; RMNH—Rijksmuseum van Natuur-Lijke Historie, Leiden; SDMNH—San Diego Museum of Natural History; UMMC—Department of Zoology, University of Miami, Coral Gables; USNM—National Museum of Natural History, Washington, D.C.

TAXONOMIC CHARACTERS

Valve Morphology

In Craspedochiton Shuttleworth, 1853, the tegmentum topography is similar to the ischnochitonid condition in possessing central and lateral areas. However, in all New World Acanthochitoninae these regions have lost their identity and usually are referred to as the combined lateropleural areas. In most Acanthochitoninae the jugum is well-differentiated, although it may be less so in cryptoplacines, Craspedochiton, and related genera. The anterior valve lacks these areas and generally is of little taxonomic importance. The posterior valve is thought to be the result of the fusion of a terminal valve, much like the anterior one, and a pre-existing intermediate valve (BERGENHAYN, 1930; STAROBOGATOV & SIRENKO, 1978), but in most cases the demarcation between these two fused valves is obscured. The posterior apex of the jugum of this fused intermediate valve persists as a distinct region on the posterior valve and is referred to as the mucro. The area posterior to the mucro is the post-mucronal slope, and its outline in profile has been used in taxonomic schemes. These morphological regions are illustrated in Figure 1.

The dominant tegmental sculpturing in the family is pustules; these correspond to esthete bodies imbedded within the pustules. Two types of esthetes of uncertain function occur in the Cryptoplacidae, and are separated here on the basis of size into macresthetes and micresthetes (Figure 2). The position of the esthetes on the pustule is of taxo-

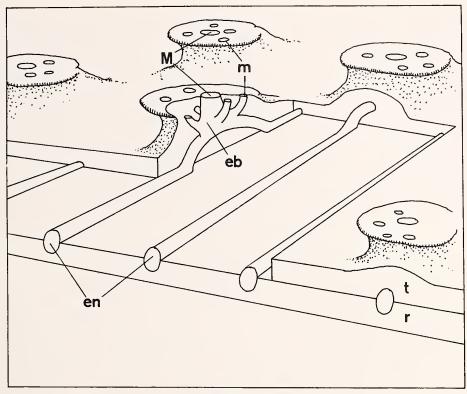


Figure 3

Esthete innervational system: diagrammatic cross-section through valve viewed from anterior growing edge. t, tegmentum; r, articulamentum; M, macresthetes; m, micresthetes; eb, esthete body; en, esthete nerves.

nomic importance. Figures 3–8 illustrate the morphology of these pustules and the relationship between the esthetes and the valve.

Girdle Elements

Cryptoplacids as a group have spiculose girdle elements, although in *Craspedochiton* these elements are flattened and scale-like. The dorsum of the girdle is covered with one or more types of spicules, which may be of taxonomic importance. Spicule types vary in sculpture (smooth or longitudinally striated), length, shape (straight or bent), and cross-sectional profile (round or flattened). In this study the term monomorphic is used to denote dorsal spicules of all one type; bimorphic refers to two distinct types of dorsal spicules that differ in any of the above regards. The determination of spicule types often requires the use of SEM or careful light microscopy examinations; gross morphological comparisons have sometimes led to erroneous conclusions (e.g., FERREIRA, 1985). An example of dorsal elements is shown in Figure 9.

Cryptoplacids typically have 18 sutural tufts, one per side at the articulation of each pair of valves and four along the anterior margin of valve I. The spicules composing these tufts are usually straight (curled in *Choneplax* Dall, 1882) and unsculptured, and vary in number from three or four to hundreds per tuft. The tufts can be "fanned-

out" or gathered together by the animal, and there is evidence that some species can partially withdraw the tufts into the girdle. Generally, variations in the tuft spicules are of limited taxonomic importance.

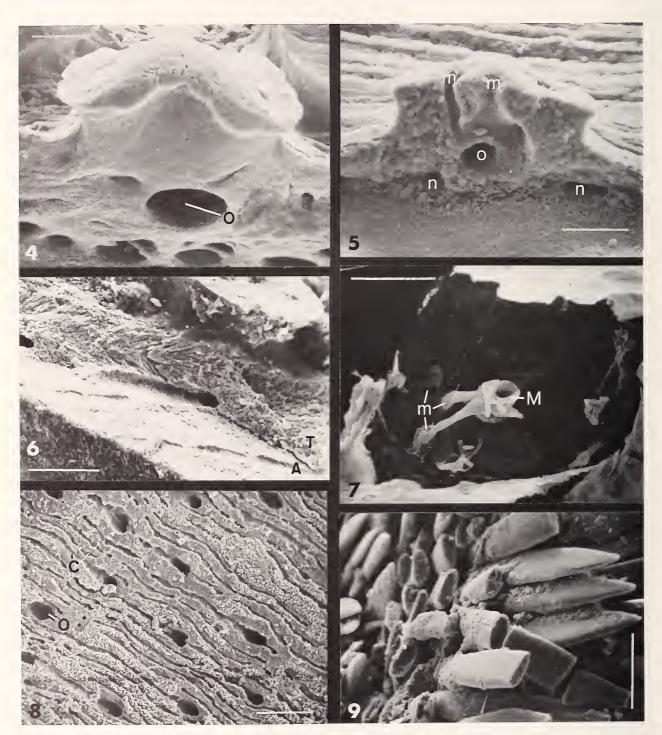
Dorsal elements may be mono- or bimorphic, straight or bent, and often sculptured with longitudinal striations. In *Acanthochitona* these elements are typically spiculose; in the cryptoplacines they are club-shaped; and in *Craspedochiton*, scale-like. Dorsal elements appear to be of taxonomic importance at the generic and specific levels.

The margin of the girdle is bounded by a fringe of spicules; these are usually flattened, monomorphic elements of little taxonomic importance.

The ventral side of the girdle is covered by small, flattened, monomorphic spicules, also of little taxonomic importance. These spicules radiate outward from the median of the animal.

Radula

The radula of chitons is a complex structure, containing 15 discrete teeth per row plus additional outer, small laterals. The largest tooth, the major lateral, has a denticle cap composed of a magnetite compound. Various degrees of taxonomic importance have been assigned to the radulae of chitons by workers, ranging from the early classifications of Thiele, based almost exclusively on radulae, to those of



Explanation of Figures 4 to 9

Figures 4-9. Cryptoplacid microstructures: valves and girdle.

Figure 4. Choneplax lata (Guilding, 1829), incompletely formed pustule at growing edge of valve. o, esthete body cavity in pustule (scale = $25 \mu m$).

Figure 5. Americhiton andersoni (Watters, 1981), incompletely

formed pustule at growing edge of valve. m, micresthetes; n, esthete nerve canals; o, esthete body cavity (scale = $20 \mu m$).

Figure 6. Acanthochitona hirudiniformis hirudiniformis (Sowerby I, 1832), fractured valve showing juncture of articulamentum (A) and tegmentum (T) with esthete nerve canals sandwiched between them (scale = $50 \ \mu m$).

Bergenhayn, whose work on fossil chitons necessarily excluded that element. In this study, as in that of BULLOCK (1988), only the denticle caps, which are easily dislodged and observed, were examined in detail. My feeling is that in the Cryptoplacidae, the radular denticle caps are too variable to be used as a species-level diagnostic, and are only marginally useful at the generic level. Representative denticle caps are illustrated for several New World species in Figures 85–93. The denticle caps of all cryptoplacids so far examined by me are tridentate, each having a medial "peg" and occasionally also possessing a smaller, lateral one.

SYSTEMATIC TREATMENT

Class Polyplacophora Gray, 1821 Order Neoloricata Bergenhayn, 1930 Suborder Acanthochitonina Bergenhayn, 1930

Family CRYPTOPLACIDAE H. &. A. Adams, 1858

Description: Small to large in size (to 10 cm in length). Tegmental sculpture of pustules or coalesced pustules, lateral and central areas weakly or not at all defined, jugal area often distinct. Jugal sinus wide and deep. Valves not overlapping in adults of some genera. Pustules containing one or more esthete bodies; esthetes present between pustules in some genera. Apophyses usually extensive and relatively thin. Intermediate valves with one slit per side; anterior valve generally with five slits; posterior valve with two or more slits, often irregularly disposed. Girdle minutely to coarsely spiculose.

Remarks: This family displays a wide range in tegmental reduction and vermiformity, and many authors have advocated the division of these chitons into two families, the Acanthochitonidae (or Cryptoconchidae) and the Cryptoplacidae. However, the presence of intermediate genera such as *Choneplax* Dall, 1882, and *Meturoplax* Pilsbry, 1894, indicates that separation into separate families is unwarranted.

Subfamily Acanthochitoninae Pilsbry, 1893

Description: Small to moderate sized species. Sculpture of pustules, rarely coalesced into ribs, jugal area well-defined. Esthetes absent from tegmentum between pustules in all species studied. Articulamentum of posterior valve

with two widely spaced slits (weak interslits occasionally present); area between slits occasionally concave. Girdle spiculose.

Remarks: This subfamily contains the following genera: Acanthochitona Gray, 1821, Bassethullia Pilsbry, 1928, Craspedochiton, Cryptoconchus Burrow, 1815, Meturoplax Pilsbry, 1894, Notoplax H. Adams, 1861, and Americhiton gen. nov.

A fossil record is known only for *Acanthochitona avicula*, which BERRY (1922) records from the Pleistocene of Santa Monica, California. I have not seen this specimen and cannot confirm its identification.

Genus Acanthochitona Gray, 1821

Acanthochitona GRAY, 1821:234. Type by monotypy, Chiton fascicularis Linnaeus, 1767; VAN BELLE, 1983:140-142 (synonymy).

Type species: Chiton fascicularis Linnaeus, 1767, by monotypy.

Diagnosis: Tegmentum sculptured with flat to concave pustules, no radial ribbing on any valve, no delineation between central and lateral areas. Jugum well-defined, smooth, or longitudinally striated. Macresthetes and/or micresthetes present on pustules and jugum but absent in interpustular spaces. Esthete innervational system sandwiched between tegmentum and articulamentum, myostracum palleale apparently absent or very reduced. Articulamentum moderately extensive. Slit formula 5-1-2+. Girdle broad relative to most chitons, encroaching on tegmentum; dorsum with dense, pointed spicules. Sutural tufts usually well-developed, marginal fringe present and conspicuous. Ventral side of girdle with fine daggerlike spicules.

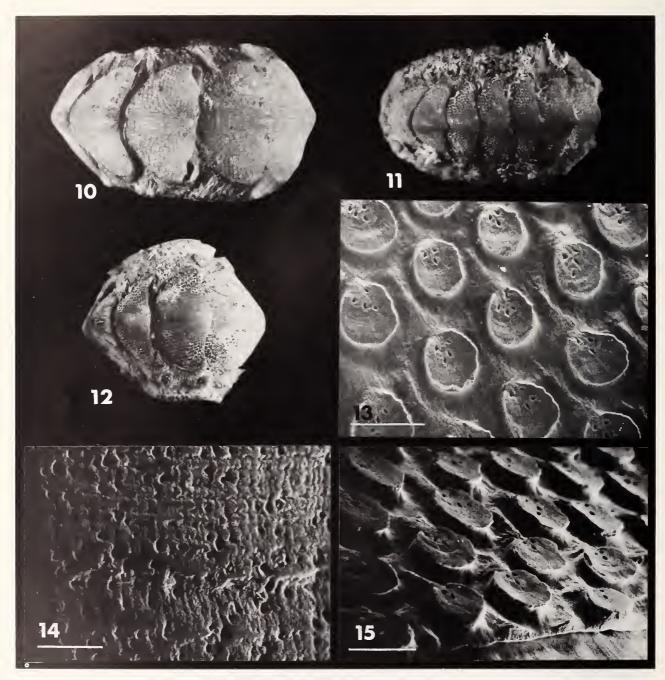
Remarks: The tegmental layer of Acanthochitona s.s. is very thin relative to that found in other studied chitons and the valves seem to lack a myostracum palleale. In the Chitoninae, this layer contains the esthete innervational system (LAGHI & RUSSO, 1979) and its absence in the acanthochitons results in the nerves being sandwiched between the tegmentum and articulamentum (this may be true of the family as a whole). The innervational system leaves its position on the tegmentum-articulamentum interface and enters the tegmentum to give rise to the esthete body proper. The typically pustulose sculpture is the direct result of the presence of these esthetes and simply represents the minimal tegmental covering over the esthete bod-

Figure 7. Acanthochitona fascicularis (Linnaeus, 1767), internal view of decalcified valve pustule. M, central macresthete; m, branching micresthetes (scale = $25 \mu m$).

Figure 8. Acanthochitona astriger (Reeve, 1847), internal view of tegmentum with articulamentum removed. Esthete nerves travel

in canals (c) between tegmentum and articulamentum until they penetrate tegmentum to form esthetes. o, esthete body cavity (scale = $100 \mu m$).

Figure 9. Americhiton andersoni (Watters, 1981), dorsal girdle elements (scale = $100 \mu m$).



Explanation of Figures 10 to 15

Figures 10-15. Acanthochitona angelica Dall, 1919.

Figure 10. Holotype of *Acanthochitona angelica* Dall, 1919, Bahía de Los Angeles, Baja California, Mexico (USNM) (11 mm, curled).

Figure 11. Paratype of *Acanthochitona jacquelinae* Smith & Ferreira, 1977, Academy Bay, Isla Santa Cruz (Indefatigable Id.), Galápagos Ids., Ecuador (AJF) (5 mm).

Figure 12. Isla Isabella, Galápagos Ids., Ecuador (ANSP) (6 mm, curled).

Figure 13. Dorsal view of pustules, Paratype of Acanthochitona jacquelinae Smith & Ferreira, 1977, Academy Bay, Isla Santa Cruz (Indefatigable Id.), Galápagos Ids., Ecuador (AJF) (scale = $100~\mu m$).

Figure 14. Dorsal view of jugum, María Magdalena Id., Mexico (AMNH) (scale = 100 μ m).

Figure 15. Oblique view of pustules, Paratype of Acanthochitona jacquelinae Smith & Ferreira, 1977, Academy Bay, Isla Santa Cruz (Indefatigable Id.), Galápagos Ids., Ecuador (AJF) (scale = $100~\mu m$).

ies (Figure 3). In Craspedochiton, Notoplax, Meturoplax, and the Cryptoplacinae, micresthetes also are found between the pustules, resulting in a thicker layer of tegmental coverage. The pustules of these groups support more esthete bodies and are convex in surface relief; in Acanthochitona s.s. the pustules are concave and rarely contain more than two macresthetes. The well-defined jugal region of Acanthochitona may be derived from a coalescing of pustules along the dorsal ridge. This smooth, fortified region may facilitate movement and resist crushing as these chitons move on the undersurfaces of rocks and shells. Some genera, such as Craspedochiton, still possess pustules in this region.

GRAY (1821) was the first worker to separate acanthochitons from Chiton, listing Chiton fascicularis Linnaeus, 1767, as his only example. Because the name was published in an obscure journal (at least to malacologists), it remained largely unnoticed, and the most widely accepted name became Acanthochites Risso, 1826; indeed, GRAY (1843) adopted a misspelling of Acanthochites rather than his own Acanthochitona. HERRMANNSEN (1846), and many of those subsequent authors who did employ Gray's name, unnecessarily emended it to conform to the endings of other chiton taxa in use at that time: Chiton, Ischnochiton, Enoplochiton, etc. ASHBY (1922:9) pointed out that "acantho" and "chiton" are both masculine and regarded Acanthochitona as a "mongrel word." However, GRAY's (1821) spelling does not constitute an incorrect original spelling and should not be emended (see ICZN Art. 32, and Iredale, 1915). Aristochiton Thiele, 1910, is a synonym of Craspedochiton s.l., not of Acanthochitona as stated by A. G. SMITH (1960).

Acanthochitona fascicularis complex

This group of species is characterized by its having proportionately broader, rectangular intermediate valves than those of the other eastern Pacific Acanthochitoninae, the *Acanthochitona hirudiniformis* complex, which tend to be more hexagonal in outline. The mucro is typically central and prominent, the sculpture is of oval to teardropshaped pustules, and the jugum is smooth or striated. The dorsum of the girdle may be covered with fine or coarse spicules; the sutural tufts are composed of fairly stout elements, fewer in number than in the *A. hirudiniformis* complex. This is a widespread complex including the common species *A. fascicularis* (Linnaeus, 1767), *A. crinita* (Pennant, 1777), and *A. zelandica* (Quoy & Gaimard, 1835).

Acanthochitona angelica Dall, 1919

(Figures 10-17, 28-30)

Acanthochitona angelica Dall, 1919:515; Keen, 1958:518; Parker, 1964:151, 166; Thorpe, 1971:866; Abbott, 1974:407; A. G. Smith, 1977:217, 254; Kaas & Van Belle, 1980:8; Watters, 1981b:173; pl. 1e-g; pl. 4e.; Lyons, 1988b:150; Skoglund, 1989:87.

Acanthochitona jacquelinae SMITH & FERREIRA, 1977:83, 93-

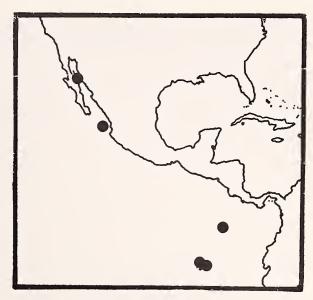


Figure 16

Distribution of Acanthochitona angelica Dall, 1919.

95; figs. 18, 19; WATTERS, 1981b:173; KAAS & VAN BELLE, 1980:67; FINET, 1985:11; SKOGLUND, 1989:88. Acanthochitona shaskyi FERREIRA, 1987:47-52; figs. 8-12; SKOGLUND, 1989:88.

"Acanthochitona cf. A. avicula (Carpenter)": SMITH & FERREIRA, 1977:95; figs. 20, 21; FINET, 1985:11.

?Acanthochitona cf. A. angelica (Dall): McLean, 1961:473.

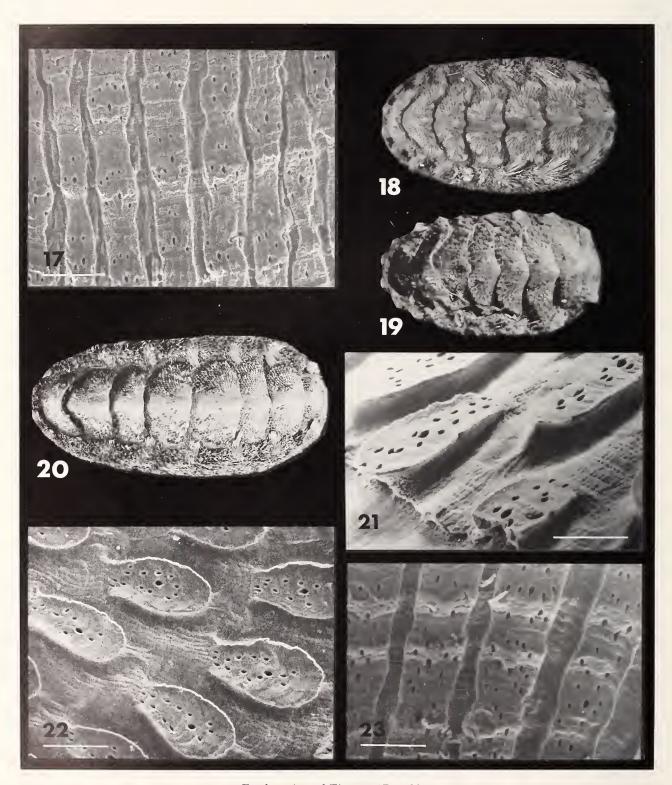
Type material: Acanthochitona angelica Dall, 1919. Holotype: USNM 110346.

Acanthochitona jacquelinae Smith & Ferreira, 1977. Holotype: CASIZ 967. Paratypes: 66 specimens, depositories unspecified. Type locality: Isla Coamaño (Jensen Id.), Galápagos Ids., in 40–60 m on broken coralline bottom.

Acanthochitona shaskyi Ferreira, 1978. Holotype: CAS-IZ 061094. Paratypes: LACM 2125; SDMNH 34359; USNM 859008; D. R. Shasky coll.; Ferreira coll. Type locality: Chatham Bay, Cocos Id., Costa Rica, in 46-69 m.

Type locality: Bahía de Los Angeles, Baja California, Mexico.

Description: Largest specimen seen, 15 mm in length. Tegmentum of intermediate valves much wider than long, moderately arched, not carinated. Beaks not prominent, posterior borders of valves nearly straight. Jugum smooth or cut with incised lines into 7–10 longitudinal striations. Jugal macresthetes arranged in longitudinal rows, each accompanied by 2–7 micresthetes. Latero-pleural areas finely pustulose, pustules oval or slightly teardrop-shaped. Each pustule bearing one macresthete located acentrically towards beak with 2–4 micresthetes confined to premacresthete area. Tegmentum uniformly orange, orange-red, brownish-red, green, white, or mottled with these colors;



Explanation of Figures 17 to 23

Figure 17. Acanthochitona angelica Dall, 1919. Dorsal view of jugum, Paratype of Acanthochitona jacquelinae Smith & Ferreira, 1977, Academy Bay, Isla Santa Cruz (Indefatigable Id.), Galápagos Ids., Ecuador (AJF) (scale = 100 µm).

Figures 18–23. Acanthochitona avicula (Carpenter, 1864). Figure 18. Ensenada, Baja California, Mexico (GTW) (13 mm).

Figure 19. Syntype of Acanthochites avicula Carpenter, 1864,

adjacent groups of valves may differ in color from other groups on same specimen.

Apophyses variable in degree of extension. Slit formula 5-1-2. Articulamentum white or white tinged with pink or orange-red towards the beak.

Girdle dorsum velvety, with bimorphic elements composed of two distinct sizes of bent spicules, both at least distally striated. Dorsum colored uniformly orange-red, dark red, greenish, white, lavender, blue, or mottled with these colors. Sutural tufts and marginal fringe well-developed, colored translucent white, yellow, blue-green, blue, or lavender.

Distribution: Gulf of California to Panama and the Galápagos Ids. This is apparently an offshore species, found to at least 50 m.

Material examined: MEXICO: BAJA CALIFORNIA: Bahía de Los Angeles (USNM); TRES MARIAS ISLANDS: María Magdelina Id. (AMNH). ECUADOR: GALÁPAGOS ISLANDS: Isla Isabella (Albemarle Id.) (ANSP); Isla Santa Cruz (Indefatigable Id.), Bahía de la Academia (AJF).

Remarks: This species has been synonymized with Acanthochitona avicula as a result of the taxonomic confusion surrounding the New World Acanthochitona. In his "Descriptions of new species of chitons from the Pacific coast of America," DALL (1919) introduced some 36 chiton species, nearly one-third of which are considered junior synonyms today. Most were insufficiently described and none was illustrated, a factor that was to render the systematics of West Coast chitons unstable for years to come. Concerning A. angelica, DALL (1919:515) stated that "from A. avicula Carpenter, it is distinguished by its more central mucro, its generally larger valves and narrower girdle." The description of A. angelica contained little information of a diagnostic nature and the species apparently has not been recognized as distinct, except by myself (WATTERS, 1981b). THORPE (1971), ABBOTT (1974), PUTMAN (1980), and KAAS & VAN BELLE (1980) all conjectured that A. angelica was synonymous with A. avicula, a conclusion that is not supported by the present data. Although A. G. SMITH (1977) was correct in saying that the sculptural differences and color patterns of A. angelica are well within the limits of the variation exhibited by A. avicula, both he and Dall failed to recognize the more salient differences in girdle ornamentation.

SMITH & FERREIRA (1977) described a new species from the Galápagos Ids., *Acanthochitona jacquelinae*, and Fer-

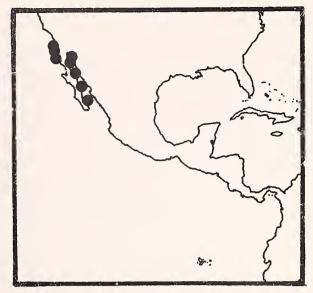


Figure 24

Distribution of Acanthochitona avicula (Carpenter, 1864).

reira kindly supplied me with paratypes. An examination of this material has revealed that A. jacquelinae is conspecific with A. angelica. The only apparent difference between the two is the smaller average size of the Galápagos specimens. SMITH & FERREIRA's (1977) observation that the sutural tufts are "unusually prominent for such a small sized chiton" (p. 93) would seem to indicate that the specimens are not mature. This is in keeping with my observation that in juvenile acanthochitons the sutural tufts are disproportionately larger than in adults.

In the same paper SMITH & FERREIRA (1977) described and illustrated specimens of "Acanthochitona cf. A. avicula" (p. 95, figs. 20, 21), also from the Galápagos Ids. From their photographs, their description of the jugal striations, and the "very small size of the spicules," these specimens are probably adults of A. angelica. They are careful to point out the differences in the girdle between A. avicula and their "Galápagos population" (i.e., A. angelica). It is perplexing that SMITH (1977), having seen Dall's type of A. angelica, did not recognize the differences in girdle ornamentation between A. angelica and A. avicula, but later, with Ferreira, carefully documented this difference in the descriptions of A. jacquelinae and "cf. A. avicula." No mention of A. angelica was made in the latter paper.

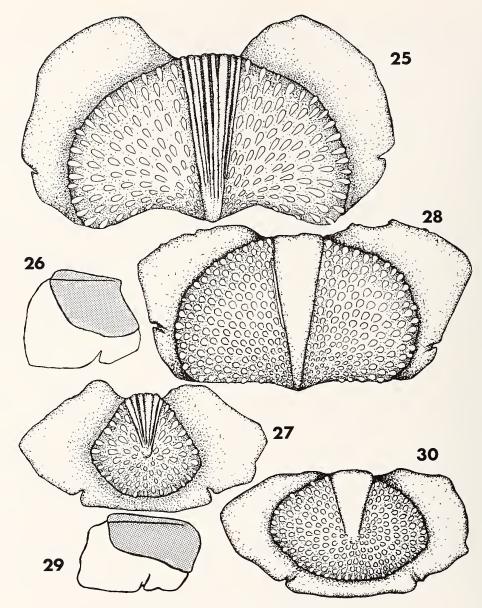
Catalina Id., California, USA (BMNH) (4.3 mm; partially disarticulated).

Figure 20. Lectotype of *Acanthochites avicula* variety *diegoensis* Pilsbry, 1893, San Diego, California, USA (ANSP) (19 mm).

Figure 21. Oblique view of pustules, Ensenada, Baja California, Mexico (GTW) (scale = $100 \mu m$).

Figure 22. Dorsal view of pustules, Ensenada, Baja California, Mexico (GTW) (scale = $100~\mu m$).

Figure 23. Dorsal view of jugum, Ensenada, Baja California, Mexico (GTW) (scale = $100 \mu m$).



Explanation of Figures 25 to 30

Figures 25–27. Acanthochitona avicula (Carpenter, 1864), Agua de Chale, Baja California, Mexico (AMNH).

Figure 25. Intermediate valve VII (3.4 mm width).

Figure 26. Posterior valve profile.

Figure 27. Posterior valve (3 mm width).

Figures 28–30. Acanthochitona angelica Dall, 1919, María Magdalena Id., Tres Marías Ids., Mexico (AMNH).

Figure 28. Intermediate valve VII (3.8 mm width).

Figure 29. Posterior valve profile.

Figure 30. Posterior valve (2.7 mm width).

Ferreira (1978) described Acanthochitona shaskyi from Cocos Id. He compared it with A. jacquelinae, finding minor differences in girdle elements and posterior valve profile. However, that species falls within the range of variation of A. angelica.

Acanthochitona angelica is the eastern Pacific cognate of the western Atlantic A. pygmaea (Pilsbry, 1893) and A.

venezuelana Lyons, 1988. From A. pygmaea, it differs in having dorsal girdle elements of two distinct sizes, both striated; in A. pygmaea these elements are of various lengths and are smooth. LYONS (1988a) does not mention any sculpture on the bimorphic spicules of A. venezuelana and compares it with A. avicula; however, as mentioned, A. venezuelana is more closely related to A. angelica. From A.

avicula, A. angelica differs in having a velvety girdle of very fine spicules rather than coarse, strongly curved elements, and in the absence of elongated pustules on the lateropleural areas. Acanthochitona imperatrix can be differentiated by its wide, flat, and smooth jugum. As with most New World acanthochitons that typically possess a striated jugum, occasional specimens may be encountered in which this structure is smooth.

Acanthochitona avicula (Carpenter, 1864)

(Figures 18-27, 88)

Acanthochites avicula CARPENTER, 1864:612, 650; CARPENTER, 1866:211; COOPER, 1867:23; CARPENTER, 1872: 98, 136; PILSBRY, 1893b:24; NIERSTRASZ, 1905:60.

Acanthochiton avicula (Carpenter): DALL, 1879a:299; pl. 4, fig. 38; DALL, 1879b:81; pl. 4, fig. 38; LELOUP, 1941:3, 9; FISCHER, 1978:37.

Acanthochitona avicula (Carpenter): DALL, 1919:515; BERRY, 1922:456, 457; STRONG, 1923:43; I. S. OLDROYD, 1927: 318, 319; STEINBECK & RICKETTS, 1941:549; BURCH, 1946:19; SMITH & GORDON, 1948:206; PALMER, 1958: 21, 31, 43, 53, 286; pl. 32, fig. 4; BURGHARDT & BURGHARDT, 1969:9; pl. 1, fig. 1; THORPE, 1971:866; fig. 11; KAAS, 1972:47; ABBOTT, 1974:407; A. G. SMITH, 1977:254; SMITH & FERREIRA, 1977:94, 95; HOUSTON, 1980:195, 196; fig. 9.230; KAAS & VAN BELLE, 1980: 13; WATTERS, 1981b:173; pl. 1h-j; pl. 4c, d; PUTMAN, 1982:366; LYONS, 1988a:97, 98, 112, 113; fig. 81; LYONS, 1988b:150; SKOGLUND, 1989:87.

Acanthochites avicula variety diegoensis PILSBRY, 1893b:25; pl. 12, figs. 52-54; NIERSTRASZ, 1905:58, 60; KAAS & VAN BELLE, 1980:38.

Acanthochiton avicula variety diegoensis (Pilsbry): Leloup, 1941:3, 9.

Acanthochites diegoensis Pilsbry: T. S. Oldroyd, 1911:73. Acanthochitona diegensis [sic] (Pilsbry): Dall, 1919:515; Lowe, 1935:32.

Acanthochitona diegoensis (Pilsbry); I. S. OLDROYD, 1927:318; BURCH, 1946:19; BURGHARDT & BURGHARDT, 1969:9; ABBOTT, 1974:407.

Acanthochites diegensis [sic] Pilsbry: STEINBECK & RICKETTS, 1941:548.

Acanthochitona avicula variety diegoensis (Pilsbry): WATTERS, 1981b:173; pl. 4d.

Acanthochitona arragonites variety diegoensis (Pilsbry): I. S. OLDROYD, 1927:318.

Non Acanthochitona cf. avicula "Carpenter," FINET, 1985:11 [=Acanthochitona angelica (Dall, 1919)].

Type material: Acanthochites avicula Carpenter, 1864. Holotype: Redpath Museum, No. 72.

Acanthochites avicula variety diegoensis Pilsbry, 1893. Lectotype: by subsequent designation of WATTERS (1981b), ANSP 349330. Type locality: San Diego, California, USA.

Type locality: Catalina Id., California, USA.

Description: Largest specimens seen, 20 mm in length. Tegmentum of intermediate valves wider than long, flattened, not carinated. Beaks prominent, jugum moderately wide, cut with deeply incised lines into 8–12 longitudinal

striations. Each jugal macresthete accompanied by 8–12 micresthetes; macresthetes on one striation not aligned with those on another. Latero-pleural areas sculptured with numerous, very elongate, teardrop-shaped pustules, with number of pustules and distance between them varying considerably between specimens. Each pustule bearing one macresthete located acentrically towards prepustular slope with 5–10 micresthetes, not confined to premacresthete area. Mucro varying in position from slightly anterior to posteriorly acentric, prominent, postmucronal slope steep and concave. Tegmentum whitish, variegated with brown, green, gray, and black; pustules often of different color than background tegmentum.

Apophyses well-developed. Slit formula (5–6)-1-2. Articulamentum white tinged with green towards the beak.

Girdle dorsum ornamented with coarse, bent spicules curving towards median, interspersed with smaller, curved spicules that become predominant towards valves. Larger spicules may be striated on distal half. Dorsum variegated with greenish-blue and cream. Sutural tufts and marginal fringe well-developed, composed of long, straight, smooth spicules, colored light green.

Distribution: Subtidally to 20 m, from southern California to Baja California Sur and the Gulf of California to Punta Cholla, Sonora, Mexico.

Material examined: USA: CALIFORNIA: San Onofree (MCZ); La Jolla, Bird Rock; La Jolla, Devil's Slide (both DMNH); La Jolla; False Bay (both AMNH); Catalina Id.; Newport Beach; San Diego, Stearn's Cove (all USNM); San Diego (AMNH, ANSP, USNM). MEXICO: SONORA: Punta Cholla (ANSP); BAJA CALIFORNIA: Ensenada (GTW); Agua de Chale (AMNH); Bahía de Los Angeles (AJF); Bahía de Los Animas (USNM); BAJA CALIFORNIA SUR: Bahía Pichilinque (USNM).

Fossil records (unconfirmed): PLEISTOCENE: California, Santa Monica, Long Wharf Canyon, Upper San Pedro Series (BERRY, 1922).

Remarks: Uncertainty of the true status of some western acanthochitons has resulted in the misidentification of perhaps two other species for *Acanthochitona avicula*: *A. angelica* certainly has been confused with it and *A. imperatrix* may also be listed in collections as *A. avicula*. Of the three species *A. avicula* appears to be the most common and probably inhabits shallower water; it is recognized by the very elongate pustules and the coarse, bent, dorsal girdle elements.

The type of *Acanthochitona avicula* is a small specimen only 4.3 mm in length, but has the characteristic sculpture and girdle elements of the more commonly seen larger individuals. PILSBRY (1893b) introduced the variety *diegoensis* for specimens having larger girdle elements, smaller pustules, and a different posterior valve profile and added (p. 25): "This may prove to be the adult form of Carpenter's *avicula*." Although the morphological differences Pils-

bry cited cannot be shown with the available material to be ontogenetic, they do fall within the range of variation of this species. Specimens depicting a wide range of variability have been found in the same locality.

Acanthochitona imperatrix Watters, 1981

(Figures 31–39, 89)

Acanthochitona sp. ?: SMITH & FERREIRA, 1977:82, 97; fig. 22.

Acanthochitona imperatrix WATTERS, 1981b:171–173; pl. 1ac; pl. 4b; Finet, 1985:11; Lyons, 1988b:150; SKOGLUND, 1989:87

Type material: Acanthochitona imperatrix Watters, 1981. Holotype: USNM 218762. Paratypes: ANSP 153484, USNM 225346.

Type locality: U.S. Fish Commission Sta. 2824, 8 fms (14.6 m) off San Diego, California, USA, 24°22′30″N, 110°19′30″W; taken with tangles on broken shell bottom, 30 April 1888, by the U.S. Fish Commission.

Description (from WATTERS, 1981b): Holotype 8.9 mm in length, curled. Tegmentum of intermediate valves about twice as wide as long, flattened, not carinated. Beaks prominent. Jugum very wide, flat, smooth, and distinctly raised above latero-pleural areas. Jugal macresthetes widely spaced, arranged in longitudinal rows, each accompanied by 0-2 micresthetes. Latero-pleural areas sculptured with numerous teardrop-shaped, close-set pustules, each moderately elevated and concave. Each pustule bearing one centrally located macresthete. Zero to five micresthetes (commonly 0) accompanying each macresthete and generally confined to area posterior to macresthete. Mucro central and prominent with concave postmucronal slope. Tegmentum uniformly peach-colored, jugum lighter. Alternating spots of cream and maroon present along posterior borders of values and flanking jugum on holotype.

Apophyses extensive. Slit formula 5-1-2. Articulamentum cream-colored, tinged with green towards beaks.

Dorsum of girdle velvety, armed with dense, very minute spicules; spicules monomorphic, round in cross-section, smooth, and slightly bent. Girdle dorsum peach-colored, ventral side slightly darker. Marginal fringe and sutural tufts well-developed in juveniles, composed of numerous long, slender spicules.

Distribution: Subtidally to at least 17 m from lower California to the Galápagos Ids. It is not endemic to the Galápagos Ids., as indicated by FINET (1985:11).

Material examined: USA: CALIFORNIA: off San Diego, U.S. Fish Commission Sta. 2824, 24°22′30″N, 110°19′30″W (USNM). MEXICO: BAJA CALIFORNIA SUR: off La Paz, U.S. Fish Commission Sta. 2826, 24°12′00″N, 109°55′00″W (USNM). ECUADOR: GALÁPAGOS ISLANDS: Isla Santa Cruz (Indefatigable Id.), Seymour Bay (ANSP).

Remarks: This species is apparently very rare in collections, although additional examples may be misidentified

in private collections as Acanthochitona avicula. It can be recognized by the wide, flat, smooth, distinctly raised jugum. The girdle elements are much finer than those of A. avicula. It is not closely related to other New World species and is placed in the A. angelica-complex with reservation. It most closely resembles A. mahensis Winckworth, 1927, from Mahé, Madras, India, and A. bisulcatus Pilsbry, 1893, from an unknown locality.

Acanthochitona hirudiniformis complex

These species are generally large, characterized by pentagonal valves, as wide as long, a low, posteriorly acentric mucro, and sculpturing with numerous small, round to oval pustules. The jugum may be smooth or striated. The dorsum of the girdle is generally covered with fine, velvety spicules; the sutural tufts are composed of many very fine spicules. In addition to Acanthochitona hirudiniformis, the complex contains the Caribbean A. astriger (Reeve, 1847), A. lineata Lyons, 1988, and A. worsfoldi Lyons, 1988, the west African A. garnoti (de Blainville, 1825), and the Hawaiian A. viridis (Pease, 1872), among others, as well as the fossil species Acanthochitona plana and Acanthochitona sp. I, both of Šulc (1934).

Placed here with some reservation are a small group of Acanthochitoninae with marked *Notoplax*-like features. They may represent an extreme expression of the *Acanthochitona hirudiniformis* complex, or possibly constitute a separate genus or subgenus of *Acanthochitona*. The group includes the Caribbean *A. hemphilli* (Pilsbry, 1893) and *A. rhodea* (Pilsbry, 1893), the eastern Pacific *A. ferreirai* Lyons, 1988, and *A. mastalleri* Strack, 1989, from the Red Sea, and probably *Notoplax eximia* Thiele, 1909, from Sulawesi.

Acanthochitona hirudiniformis hirudiniformis (Sowerby I, 1832)

(Figures 40-50, 53-59, 92)

Chiton hirudiniformis Sowerby I (in Broderip & Sowerby I), 1832:59; Sowerby II, 1840:7; figs. 23, 142; Adams, 1847:25; d'Orbigny, 1847:484.

Chiton hirudinifomis [sic] Sowerby I: REEVE, 1847:pl. 10, fig. 54.

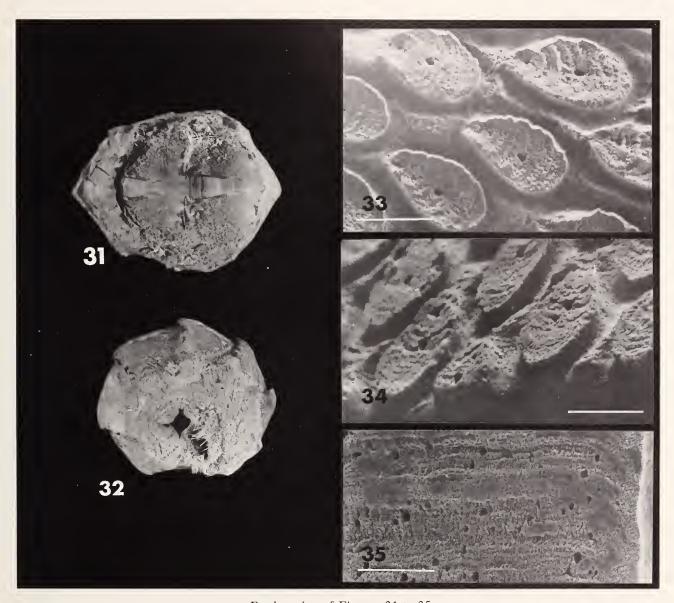
Phakellopleura (Acanthochites) hirundiniformis [sic] (Sowerby I): SHUTTLEWORTH, 1853:206, 207.

Acanthochites hirudiniformis (Sowerby I, 1832): WIMMER, 1879:506; STEARNS, 1893:410; PILSBRY, 1893b:27; pl. 2, figs. 49, 56; PILSBRY & VANATTA, 1902:552; NIERSTRASZ, 1905:61; THIELE, 1908:17; DALL, 1909:246; THIELE, 1909:4.

Acanthochiton hirudiniformis (Sowerby I): HADDON, 1886:35, 36; THIELE, 1893:398; pl. 32, fig. 30; LELOUP, 1941:1; LELOUP, 1956:5, 27-29, 86, 88, 89, 92; fig. 8.

"?Tonicia hirudiniformis (Sowerby)": STEARNS, 1893:449. Chiton (Acanthochites) hirudiniformis Sowerby I: Clessin, 1904:59; pl. 22, fig. 2.

Chiton hyrundiniformis [sic] Sowerby I: CLESSIN, 1904:59.
Chiton (Acanthochites) hirudiformis [sic] Sowerby I: CLESSIN, 1904:59.



Explanation of Figures 31 to 35

Figures 31-35. Acanthochitona imperatrix Watters, 1981.

Figures 31, 32. Holotype of *Acanthochitona imperatrix* Watters, 1981, San Diego, California, USA (USNM) (8.9 mm, greatest dimension of curled individual).

Figures 33-35. Paratype of Acanthochitona imperatrix Watters, 1981, San Diego, California, USA (USNM).

Acanthochitona hirundiniformis [sic] (Sowerby I): DALL, 1919: 515; FINET, 1985:11.

Acanthochitona hirudiniformis (Sowerby I): Hertlein, 1963: 242; Thorpe, 1971:866, 868; fig. 13; Smith & Ferreira, 1977:82, 92, 93, 95; fig. 17; Kaas & Van Belle, 1980: 60; Watters, 1981a:77; Lyons, 1988a:87, 91, 92, 98, 112, 113; figs. 52–56; Skoglund, 1989:87.

Acanthochitona hirudiniformis hirudiniformis (Sowerby I): WATTERS, 1981b:173.

Acanthochitona panamensis "Pils.": PILSBRY & LOWE, 1932: 130 [nomen nudum]; KAAS & VAN BELLE, 1980:95.

Figure 33. Dorsal view of pustules (scale = $100 \mu m$).

Figure 34. Oblique view of pustules (scale = $100 \mu m$).

Figure 35. Dorsal view of jugum (scale = $100 \mu m$).

Acanthochiton coquimboensis Leloup, 1941:1-4; fig. 1; pl. 1, fig. 1; Kaas & Van Belle, 1980:31.

Acanthochitona coquimboensis (Leloup): Thorpe, 1971:866; SMITH & FERREIRA, 1977:93; KAAS & VAN BELLE, 1980: 31; WATTERS, 1981b:173.

Acanthochitona tabogensis A. G. SMITH, 1961:87; pl. 9, fig. 1 [new name for A. panamensis Pilsbry & Lowe, 1932]; THORPE, 1971:886; SMITH & FERREIRA, 1977:93; KAAS & VAN BELLE, 1980:129; WATTERS, 1981b:173; LYONS, 1988a:82.



Figure 36

Distribution of Acanthochitona imperatrix Watters, 1981.

"Chiton (Radsia) stokesii," BIOLLEY, 1907:24 [non Broderip, 1832, fide HERTLEIN, 1963:242].

Non Acanthochites hirudiniformis "Pilsbry," DUNKER, 1882: 160 [?=Acanthochitona rubrolineata (Lischke, 1873)].

Non Acanthochiton hirudiniformis "Sowerby," STUARDO, 1959: 143, 145 [=Acanthochitona hirudiniformis peruviana (Leloup, 1941)].

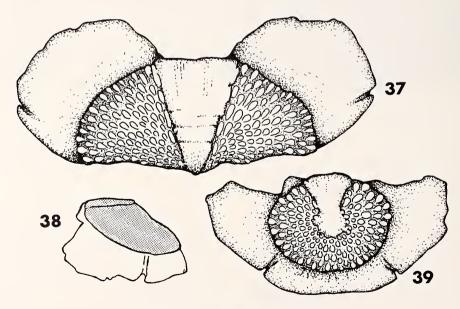
Type material: *Chiton hirudiniformis* Sowerby I, 1832. Syntypes: BMNH 1984050.

Acanthochiton coquimboensis Leloup, 1941. Syntypes: BMNH 1886.6.9.705; originally three specimens, the illustrated specimen (pl. 1, fig. B) cannot be located (in litt., S. Morris, 21 March 1989). Type locality: Coquimbo, Peru.

Acanthochitona tabogensis A. G. Smith, 1961. Holotype: SDMNH 23666. Type locality: Taboga Id., western Panama.

Type locality: "ad littora Peruviae (Ançon, Lobos Island, and Payta), et ad insulis Gallapagos (Chatham Island)," restricted by SMITH & FERREIRA (1977) to Chatham Id. (Isla San Cristobal), Galápagos Ids., Ecuador; restored here to Sowerby's original type locality (see below).

Description: Largest specimen seen, 36 mm in length, strongly curled. Tegmentum of intermediate valves about as wide as long, pentagonal in outline. Beaks not prominent. Jugum smooth except for growth lines in northern populations, but longitudinal striations may occur in south. Some southerly individuals may alternate between striated and non-striated jugal sculpture. Jugal macresthetes arranged in irregular longitudinal rows, each accompanied by 3–6 micresthetes. Latero-pleural areas sculptured with numerous oval or teardrop-shaped pustules, each pustule bearing one centrally located macresthete and 0–4 micresthetes confined to premacresthete area. Mucro central, not prominent, postmucronal slope straight or convex. Tegmentum uniformly colored dark greenish-brown, many mainland specimens with paler bands parallel to jugum.



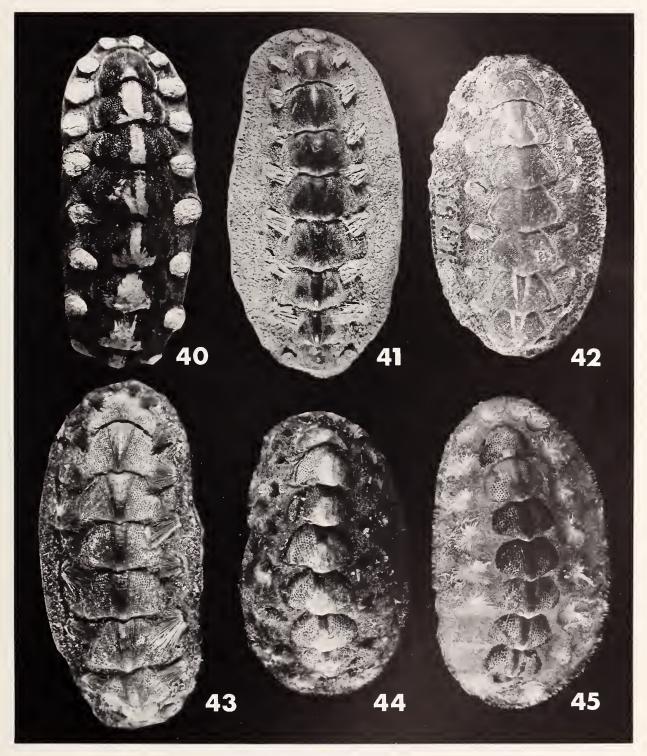
Explanation of Figures 37 to 39

Figures 37–39. Paratype of Acanthochitona imperatrix Watters, 1981, San Diego, California, USA (USNM).

Figure 37. Intermediate valve VII? (3.9 mm width).

Figure 38. Posterior valve profile.

Figure 39. Posterior valve (2.8 mm width).



Explanation of Figures 40 to 45

Figures 40-45. Acanthochitona hirudiniformis hirudiniformis (Sowerby I, 1832).

Figure 40. Syntype of Acanthochiton coquimboensis Leloup, 1941 (BMNH) (16.9 mm).

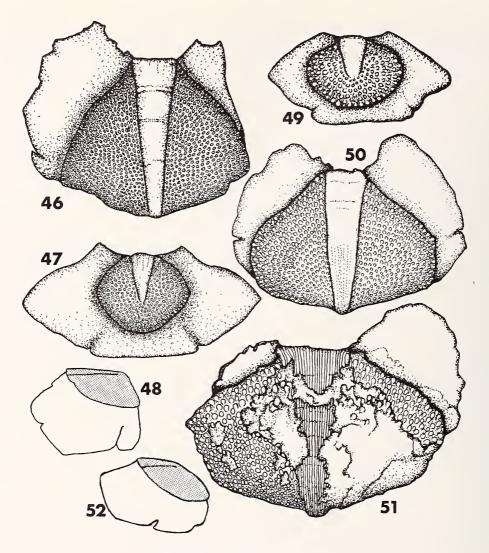
Figure 41. Syntype of *Chiton hirudiniformis* Sowerby I, 1832 (BMNH) (26.5 mm).

Figure 42. Holotype of Acanthochitona tabogensis A. G. Smith, 1961, Taboga Id., Panama (SDMNH) (30 mm).

Figure 43. Isla Pinzón (Duncan Id.), Galápagos Ids., Ecuador (GTW) (20 mm).

Figure 44. Flamenco Id., Canal Zone (RCB) (20 mm).

Figure 45. Flamenco Id., Canal Zone (RCB) (25 mm).



Explanation of Figures 46 to 52

Figures 46-48. Acanthochitona hirudiniformis (Sowerby I, 1832), Isla Pinzón, Galápagos Ids., Ecuador (GTW).

Figure 46. Intermediate valve VII (6 mm width).

Figure 47. Posterior valve (6 mm width).

Figure 48. Posterior valve profile.

Figures 49–50. Acanthochitona hirudiniformis (Sowerby I, 1832), San Juan del Sur, Nicaragua (SDMNH).

Apophyses well-developed. Slit formula 5-1-2. Articulamentum flushed with green, brownish towards beaks.

Girdle dorsum densely covered with needlelike spicules. In northern part of range, dorsal elements monomorphic, smooth, and slightly bent; in southern populations, larger, stouter, straight element may be found interspersed among smaller elements characteristic of north. New element may or may not be striated. Girdle dark green in color. Sutural tufts and marginal fringe may be well-developed; bronze in color. Worn specimens may be devoid of spicules.

Figure 49. Posterior valve (4 mm width).

Figure 50. Intermediate valve V (5.5 mm width).

Figures 51, 52. Acanthochitona hirudiniformis peruviana (Leloup, 1941), Valparaiso, Chile (USNM).

Figure 51. Intermediate valve VII (3.9 mm width).

Figure 52. Posterior valve profile.

Distribution: Intertidally to at least 2 m from the Gulf of California through western Central America to Peru and the Galápagos Ids. Lyons (1988a:92) states that this species occurs "intertidally on high energy rocky shores."

Material examined: MEXICO: BAJA CALIFORNIA: Bahía Las Animas (USNM). NICARAGUA: Puerto San Juan del Sur (ANSP). Costa RICA: Bahía Huevos (ANSP); Bahía Cocos (DMNH). PANAMA: Tonosi Búcaru (AMNH); Isla Tobago (ANSP, SDMNH); Punta Patilla (GTW); Cam-

eron (AMNH); Punta Mala (RCB); Naos Id.; Punta del Toro; Pearl Id. (all USNM). Canal Zone: Flamenco Id.; Culebra Id. (both RCB). Peru: (AMNH, ANSP); Payta (MCZ). Ecuador: Galápagos Islands: Isla Fernandina (Narborough Id.); Isla Isabella (Albemarle Id.), Tagus Cove (both ANSP); Isla San Salvador (James Id.) (MCZ); Isla Pinzón (Duncan Id.) (ANSP, DMNH, GTW); Isla Santa Cruz (Indefatigable Id.), Bahía de la Academía (AMNH, DMNH, GTW, USNM); Isla Santa Fé (Barrington Id.) (AMNH); Isla Santa María (Charles Id.) (MCZ).

Fossil records: None reported.

Remarks: Sowerby I (1832) based his description of Acanthochitona hirudiniformis on a series of specimens from Ançon, Lobos Id., and Payta (all Peru) and Chatham Id., Galápagos Ids., Ecuador. The variation of this species and the broad range of Sowerby's type locality has caused subsequent workers to puzzle over exactly how many taxa were included in Sowerby's syntype lot, and which one(s) actually represented A. hirudiniformis. LELOUP (1941), working with a very small sample of Peruvian specimens, described two new species: A. peruviana and A. coquimboensis. Neither was compared with A. hirudiniformis, though Leloup did state that A. coquimboensis differed from it "sous tous rapports" (p. 1). Thorpe (1971) synonymized Leloup's two species with A. hirudiniformis but gave no reason for this action. SMITH & FERREIRA (1977) questioned Thorpe's conclusions and suspected that several taxa were involved; they believed that consistent differences appeared to exist between Galápagos and mainland populations, particularly in the size of the pustules and the morphology of the girdle elements. For this reason they restricted the type locality of A. hirudiniformis to Chatham Id., as suggested by Pilsbry in manuscript. They suggested that the mainland forms, if indeed different, may be allocated to one (or both) of Leloup's names or to Smith's A. tabogensis (1961), described from the Bay of Panama. This was an unfortunate action for the following reasons. The syntype lot contains specimens from four different localities, but there is no indication of which specimen is from which locality. SMITH & FERREIRA (1977) restricted the type locality but did not select a lectotype; in fact they could not select one. Thus a situation was created in which the type locality could not be paired with any specimen of the syntype lot. Conversely, I cannot designate a lectotype corresponding to the Ecuadorian locality. ICZN rules do not address this issue. I feel that it is best to reject Smith and Ferreira's type locality restriction and to restore the type locality to Sowerby's original broad range. For these same reasons, I have not designated a lectotype for this species.

PILSBRY & LOWE (1932:130), in a list of mollusks from west Mexico and Central America, recorded "Acanthochitona panamensis Pils. Under stones at extreme low tide, quite rare. Taboga Island; Montijo Bay; San Juan del Sur." This name was never officially introduced and is a

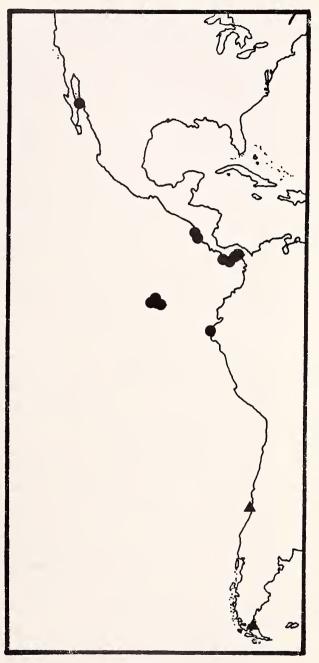
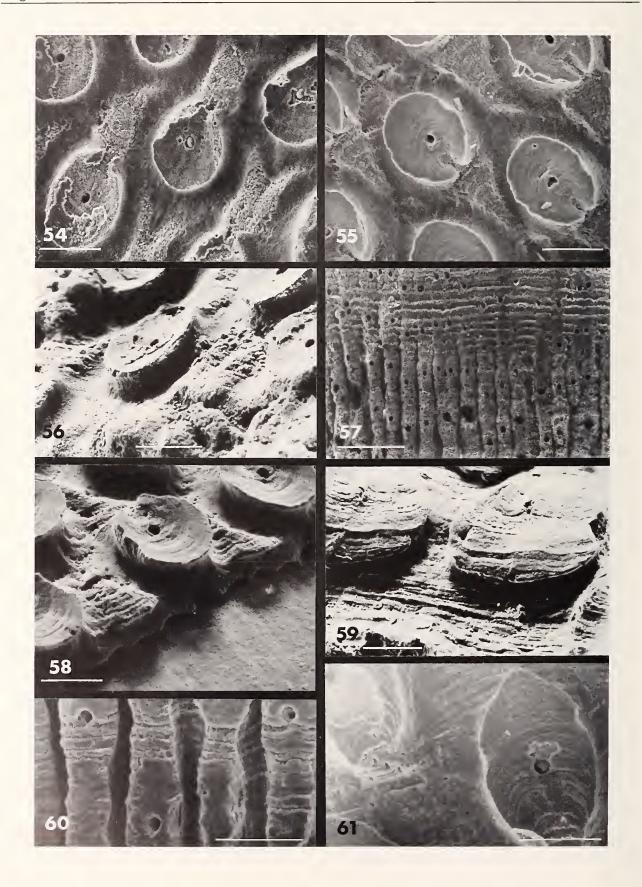


Figure 53

Distribution of Acanthochitona h. hirudiniformis (Sowerby I, 1832) (•) and Acanthochitona h. peruviana (Leloup, 1941) (•).

nomen nudum. A. G. SMITH (1961), working with Pilsbry's proposed type of *A. panamensis* (ANSP 153556), and additional material from Nicaragua, introduced this species under the name *A. tabogensis* from Taboga Island. However, additional lots of "*A. tabogensis*" (SDMNH 23659), identified as such by Smith, are examples of *A. ferreirai*.

In addition to Acanthochitona coquimboensis, A. peruvi-



anus, A. panamensis, and A. tabogensis, two other names (both nomen nuda) were proposed for local variants of A. hirudiniformis, and exist in collections, but were never introduced. Examination of the material at the Museum of Comparative Zoology yielded "Acanthochiton hassleri Cpr. type" from Payta, Peru, collected by the Hassler Expedition (MCZ 1260 and another unnumbered lot). The Academy of Natural Sciences collection contains a lot, ANSP 35788, of one whole and one broken, disarticulated specimen of a very large acanthochiton (36 mm in length, strongly curled) labeled as type and paratype of "A. inca Pilsbry MS" from Peru (non Chiton inca d'Orbigny, 1841, or von Wissel, 1904). SMITH & FERREIRA (1977) stated that the ANSP specimens were purchased in London between 1846 and 1849, probably from Hugh Cuming. Both "A. hassleri" and "A. inca" differ from Galápagos and Central American specimens primarily in possessing large, stout, dorsal girdle elements among the finer, more numerous elements typical of northern populations.

Acanthochitona hirudiniformis extends along the coast of the western New World from Baja California to Tierra del Fuego in a narrow longitudinal range. Although breeding theoretically can occur between members throughout the entire range, it is far less likely that northern and southern individuals interbreed than do contiguous segments of the population. The results may be a north-tosouth cline in characteristics, in particular girdle element composition and jugal sculpture. Northern populations possess only needlelike dorsal elements, while in Peru stout, blunt spicules appear occasionally among them. From Chile south the stout elements appear almost exclusively of the needlelike spicules. Northern populations have a smooth jugum while southern individuals have only striated jugums; Peruvian examples may have both striated and nonstriated jugal regions on the same individual (Figure 57). Although specimens south of Peru are extremely rare in collections, the few available seem to be homogeneous in their characteristics. The regions north and south of Peru may be interpreted as a pronounced clinal step and the two populations considered as subspecies (MAYR, 1969): A. h. hirudiniformis in the north and A. h. peruviana in the south. I cannot find sufficient differences to warrant the separation of the Galápagos Ids. population from the mainland individuals. The variability of this species throughout its range has resulted in the several aforementioned names applied to local variants; only two subspecies are recognized here. They may have arisen as the result of the South Equatorial Current, which originates off the coast of Peru, dividing the western coast of South America in two at that point. BULLOCK (1988) found that *Chiton magnificus* Deshayes, 1827, was also divided into north and south subspecies along western South America, although not at this point.

Acanthochitona h. hirudiniformis, particularly Peruvian specimens, may be confused with A. h. peruviana. Although the Peruvian examples of the former may possess the stout girdle elements of A. h. peruviana, the predominant elements on the dorsum are the slender, needlelike spicules of the more northern specimens. This species is most similar to several Caribbean taxa: A. astriger (Reeve, 1847), which possesses slightly finer and straighter dorsal elements, A. worsfoldi Lyons, 1988, a much smaller species with very fine dorsal elements and fewer sutural tuft spicules, and A. lineata Lyons, 1988, which has relatively larger tegmental pustules and longer dorsal elements.

Acanthochitona hirudiniformis peruviana (Leloup, 1941)

(Figures 51-53, 60, 61)

Acanthochiton peruviana LELOUP, 1941:6-9; figs. 4, 5; pl. 1, fig. 3; KAAS & VAN BELLE, 1980:99.

Acanthochiton peruviana (Leloup): THORPE, 1971:866.
Acanthochitona hirudiniformis peruviana (Leloup): WATTERS, 1981b:173.

Acanthochiton hirudiniformis "Sowerby": STUARDO, 1959:143, 145.

Acanthochitona sp.: Smith & Ferreira, 1977:93.

Type material: Acanthochiton peruviana Leloup, 1941. Holotype: Musée royal d'Histoire naturelle de Belgique.

Type locality: "Perou."

Description: Largest specimen, 23 mm in length. Tegmentum of intermediate valves pentagonal in outline, flat-

Explanation of Figures 54 to 61

Figures 54-59. Acanthochitona hirudiniformis hirudiniformis (Sowerby I, 1832).

Figure 54. Dorsal view of pustules, Cameron, Panama (AMNH) (scale = $100 \mu m$).

Figure 55. Dorsal view of pustules, Punta Patillo, Panama (GTW) (scale = $100 \mu m$).

Figure 56. Oblique view of pustules, Cameron, Panama (AMNH) (scale = $100 \mu m$).

Figure 57. Dorsal view of jugum, Cameron, Panama (AMNH) (scale = $100 \mu m$).

Figure 58. Oblique view of pustules, Punta Patillo, Panama (GTW) (scale = $100 \mu m$).

Figure 59. Oblique view of pustules, "Peru" (ANSP) (scale = $100 \mu m$).

Figures 60, 61. Acanthochitona hirudiniformis peruviana (Leloup, 1941), Valparaiso, Chile (USNM).

Figure 60. Dorsal view of jugum (scale = $100 \mu m$).

Figure 61. Dorsal view of pustules (scale = $100 \mu m$).

tened, not carinated. Beaks prominent. Jugum cut by numerous (ca. 20) finely incised, longitudinal striations that appear granulose. Jugal macresthetes arranged in single rows per striation, with no accompanying micresthetes. Latero-pleural areas finely pustulose, pustules oval to teardrop-shaped. Each pustule bearing one centrally located macresthete with 2–6 micresthetes distributed on pustule or confined to prepustular slope. Mucro posteriorly acentric, fairly prominent, post-mucronal slope convex. Tegmentum uniformly white, greenish-brown, or brown, with scattered flecks of lighter shades. Jugum may be darker in color and paralleled by lighter band on each side.

Apophyses moderately extensive. Slit formula 5-1-2. Articulamentum white, tinged with rose towards beaks.

Girdle dorsum covered with large, coarse, striated spicules between which may be much smaller, smoother elements. Girdle greenish-gray or greenish-brown; coarse elements with tan or dark green tips. Sutural tufts and marginal fringe not complete in known examples but appear to be composed of numerous, needlelike spicules.

Distribution: The records of the few known specimens indicate a patchy distribution from Peru to Tierra del Fuego; nothing is known of this bathymetric range. With the exception of *Acanthochitona fascicularis*, which may have been fortuitously introduced to Tierra del Fuego (USNM; BMNH), and *Notoplax magellanica* Thiele, 1909, which I have not seen, this is the most southern species of the family in the New World.

Material examined: CHILE: Valparaiso; Tierra del Fuego, Orange Harbour (both USNM).

Remarks: LELOUP (1941) described this species based upon a single specimen in the Musée royal d'Histoire naturelle de Belgique labeled "Chiton limaciformis Sow. Perou, coll. Haas." I have located two additional specimens of this rare species in the U.S. National Museum of Natural History, both very poorly preserved.

The better preserved of the two (USNM 5804) is an entire, curled individual that at some time had been glued to a card or box. Much of the girdle has been worn away so that the only intact section of the girdle is the part that had been covered with glue. A series of labels accompany the specimen. The first bears the inscription "5804 Acanthochiton" on a U.S. Exploring Expedition label annotated "Orange Harbor, Patagonia, South America." A second label reads: "Acanthochiton sp. ind. The specimen sent in the box was Phakellopleura violacea." On the same label in different ink is the notation "Orange Har.? Sent as the type of Ch. viridulus Gld.-Pl. 27, f. 413 but does not resemble the specimen figured" and is signed with Carpenter's initials. A third label reads "5804 Acanthochites hirudiniformis Sby. Orange Harbor, Patagonia, U.S. Ex. Exp." The coloration of the specimen and the naked girdle could result in the misidentification of this individual for Phakellopleura violacea [=Notoplax violaceus (Quoy & Gaimard, 1835)]. I suspect that the specimen was sent labeled

as Chiton viridulus [=Ischnochiton viridulus (Gould, 1846)]. Carpenter, upon finding the specimen to be in disagreement with published figures, reidentified it (erroneously) as *P. violaceae*. At some subsequent time it was again reidentified as *A. hirudiniformis*.

The second specimen (USNM 19284) from Valparaiso, also collected by the U.S. Exploring Expedition, is disarticulated with the valves broken, weathered, and bleached. The girdle is nearly devoid of spicules. It was identified as A. "hirundiniformis" [sic] by Carpenter.

SMITH & FERREIRA (1977:93) discussed both of these specimens under the "remarks" section of *Acanthochitona hirudiniformis*. They concluded that these chitons "probably represent other species." Thorpe (1971) placed *A. peruviana* in synonymy with *A. hirudiniformis* without presenting evidence for this conclusion.

Acanthochitona h. peruviana represents one of the rarest species of New World acanthochitons in collections. Its rarity, however, is probably not due to the inaccessibility of the western South American-Patagonian region for collecting, as numerous reports on the Chilean-Magellanic chitons have been published that make no mention of an acanthochiton: Frembly, 1827; Thiele, 1906, 1911; Melvill & Standen, 1912; Bergenhayn, 1937; Leloup, 1937, 1956, 1980; Castellanos, 1948, 1951, 1956; Barattini, 1951; Carcelles, 1950, 1953; Carcelles & Williamson, 1951; Stuardo, 1959, 1964. Other accounts report A. stygma and A. conthouyi, both de Rochebrune, 1889. I believe A. stygma to be the leptochitonid Hemiarthrum setulosum Dall, 1876, and Kaas & Van Belle (1980, 1985) believe A. couthouyi also to be that species.

Acanthochitona ferreirai Lyons, 1988

(Figures 62–66)

Acanthochitona rhodea KEEN, 1958:519; fig. 10 [in part]; A. G. SMITH, 1961:89; THORPE, 1971:867, 868; fig. 14; BULLOCK, 1974:164 [in part]; FERREIRA, 1985:207, 208 [in part] [non Pilsbry, 1893].

Acanthochitona ferreirai Lyons, 1988a:79, 85, 86, 112, 113; figs. 19-24; SKOGLUND, 1989:87.

? Acanthochites rhodeus Pilsbry: NIERSTRASZ, 1905:60.

Type material: Acanthochitona ferreirai Lyons, 1988. Holotype: USNM 859314; no paratypes were available for study.

Type locality: Punta Mala, [western] Panama.

Description (from Lyons, 1988a:85, 86): Largest specimen (holotype), 28.2 mm long, 17.0 mm wide, including girdle; valves occupying approximately 65% of total specimen width. Exposed valves uniformly red or rose, usually with white maculations; unexposed parts rose pink. Girdle broad, orange-brown or dark red, with large white patches of spicules unevenly spread across dorsal surface; spicules of dorsal tufts green.

Valve i semilunate, wider than long, concave posteriorly, with anterior insertion plate bearing 5 slits; tegmentum



Explanation of Figures 62 and 63

Figures 62, 63. Acanthochitona ferreirai Lyons, 1988. Figure 62. Holotype of Acanthochitona ferreirai Lyons, 1988, Punta Mala, Panama (USNM) (28.2 mm).

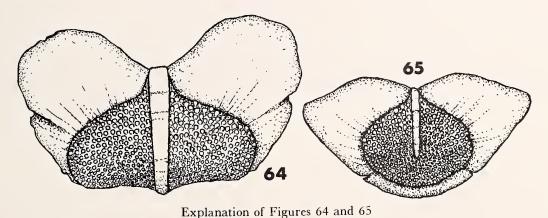
Figure 63. San Juan del Sur, Nicaragua (SDMNH) (25 mm).

occupying about 65% total valve length. Valves ii–vii beaked; tegmentum alate, twice as wide as long, constricted anteriorly, with anteriolateral margins concave near jugum; sutural laminae broad, flared anterolaterally, separated anteriorly by wide, shallow sinus; lateral areas near midpoints of margins. Valve viii broadly triangular, twice as wide as long, rounded posteriorly, with nearly central mucro; tegmentum ovate, wider than long, constricted anteriorly along jugum; sutural laminae very wide, flared anterolaterally, with straight anterior margins, separated by very shallow, broad, V-shaped sinus; 2 slits in posterior insertion plate small, narrow, V-shaped.

Jugum smooth, narrow, with parallel sides well-separated from lateral tegmentum surface, extended anteriorly beyond main tegmentum mass. Tegmentum of all valves covered with small (100 μ m) round to slightly ovate pustules, with subcentral macresthete, 3–4 micresthetes.

Girdle upper surface covered with dense mat of very small (60 μ m) spicules overlain by extensive patches of slender, straight, white spicules 400–500 μ m long, especially evident posteriorly and where girdle intrudes between valves; 18 anterior and sutural tufts containing 50–60 straight or slightly curved, stout, sharp-tipped green spicules up to 2.2 mm long; margin fringed with slender, sharp-tipped spicules up to 1 mm long, arranged in alternating groups of purple and white; underside densely covered with slender, sharp-tipped spicules about 80–90 μ m long, directed toward periphery.

Distribution: Lyons (1988a:85) gave the distribution as the "Pacific coasts of Costa Rica and Panama; intertidal and shallow subtidal depths." It apparently extends north as far as Sonora, Mexico; records from Peru have not been substantiated.



Figures 64, 65. Acanthochitona ferreirai Lyons, 1988, Punta Mala,

Panama (FSBC). Redrawn from Lyons (1988a). Figure 64. Intermediate valve IV (ca. 23 mm).

Figure 65. Posterior valve (ca. 11 mm).



Figure 66

Distribution of Acanthochitona ferreirai Lyons, 1988.

Material examined: Mexico: Sonora: Guaymas (AJF). Nicaragua: San Juan del Sur (SDMNH). Costa Rica: Puerto Quepos; Playa de Jaco, Puntarenas (both AJF). Panama: Punta Mala (RCB, USNM). Canal Zone: Flamenco Id. (RCB).

Remarks: This species, and its congeners Acanthochitona rhodea and A. hemphilli, both of PILSBRY, 1893, have been the subject of considerable confusion. Historically, A. hemphilli has been considered the Caribbean species and A. rhodea the eastern Pacific taxon, without much evidence to support this contention. In 1980 I considered (unpublished M.S. Thesis) the two to be conspecific (including the third, then undescribed species, A. ferreirai); I was followed in this decision by FERREIRA (1985). LYONS (1988a) has determined that A. rhodea and A. hemphilli are good species and are confined to the western Atlantic; he described the remaining eastern Pacific taxon, A. ferreirai, as new. I doubt that these taxa are distinct, but in lieu of more material from the eastern Pacific, I retain A. ferreirai as a valid species.

Acanthochitona rhodea and A. hemphilli were not originally described by Pilsbry in the 15th volume of the Manual of Conchology in 1893 as stated by Kaas & Van Belle (1980) and Lyons (1988a). That section was issued 16 November 1893 (fide Vanatta, 1927, and Boss et al., 1968); both species were described by Pilsbry in the July (possibly August) number of The Nautilus earlier that same year (Clench & Turner, 1962).

This large chiton cannot be confused with any other eastern Pacific species; the brick-red color of the tegmentum and girdle, the encroachment of the girdle on the valves, and the leathery aspect of the girdle separate this from sympatric species. Only *Acanthochitona exquisita* also possesses a high degree of girdle encroachment, but that species has an olive-green girdle and tegmentum and enormously produced sutural tufts. From the original description, *Notoplax eximia* Thiele, 1909, from Cape Rivers, Celebes (=Sulawesi), appears to be extremely close to this New World group.

Acanthochitona exquisita (Pilsbry, 1893)

(Figures 67-76, 93)

Acanthochites exquisitus PILSBRY, 1893a:32; PILSBRY, 1893b: 23; pl. 12, figs. 44-47; PILSBRY, 1893c:95, 96; NIERSTRASZ, 1905:60.

Acanthochitona exquisita (Pilsbry): Dall, 1919:515; Pilsbry & Lowe, 1932:130; Lowe, 1933:112; Steinbeck & Ricketts, 1941:220, 549, 551, 556; pl. 27, fig. 1; M. Smith, 1944:70; Keen, 1958:519; fig. 9; McLean, 1961: 453, 454, 456, 473; Dushane, 1962:50; Parker, 1964: 151, 166; Coan, 1968:130; Dushane & Sphon, 1968: 235, 244; Thorpe, 1971:866; fig. 12; Dance, 1973:42, 43; fig. 3; Houston, 1973:178; fig. 6.75; Abbott, 1974: 407; Houston, 1980:195; fig. 9.229; Kaas & Van Belle, 1980:45; Watters, 1981b:173; Abbott & Dance, 1982: 287; 1 fig.; Skoglund, 1989:87.

Acanthochiton exquisitus (Pilsbry): Leloup, 1941:4-6; figs. 2, 3; pl. 1, fig. 2; FISCHER, 1978:37.

Acanthochites exquisitus variety ampullaceus PILSBRY, 1893b: 24; pl. 4, fig. 85; NIERSTRASZ, 1905:60.

Acanthochiton exquisitus variety ampullaceus (Pilsbry): LELOUP, 1941:6.

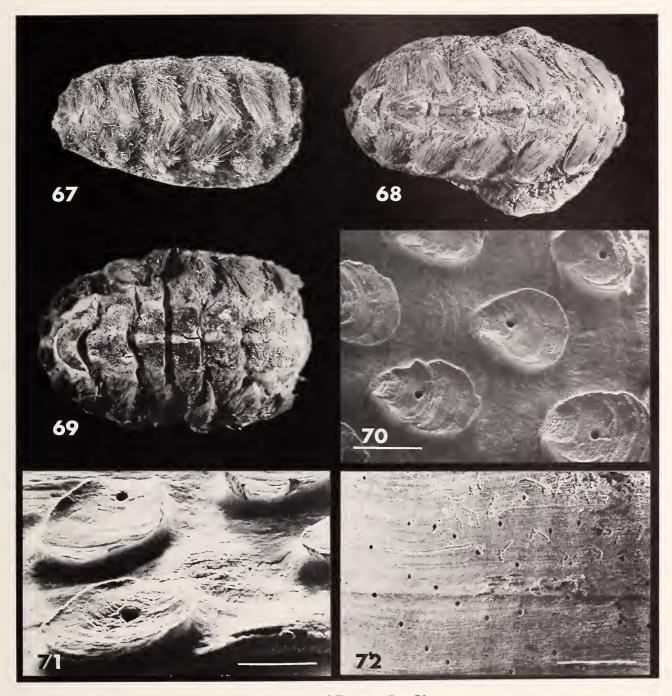
Acanthochitona exquisita ampullacea (Pilsbry): Kaas & Van Belle, 1980:45.

Type material: Acanthochites exquisitus Pilsbry, 1893. Lectotype: herein designated (ANSP 349332).

Acanthochites exquisitus variety ampullaceus Pilsbry, 1893. Lectotype: herein designated (ANSP 349329). Type locality: La Paz (Baja California Sur, Mexico).

Type locality: Las Animas Bay, Baja California, Mexico. In the original description of *Acanthochitona exquisita*, PILSBRY (1983a) gave the type locality as La Paz (Baja California Sur, Mexico), but later (1893c) stated that that information was in error and corrected the type locality to Las Animas Bay (in accordance with ICZN Art. 72H (b)). This correction has been overlooked by other workers. The type locality of the syntype lot of *A. e. ampullaceus* was also given as La Paz but PILSBRY did not mention in his 1893c paper whether this type locality designation was also erroneous. It is possible that Pilsbry extracted the syntypes of *A. e. ampullaceus* from a series of *A. exquisita* from Las Animas, but in lieu of more information, the type locality of *A. e. ampullaceus* must stand as La Paz.

Description: Largest specimen, 47 mm in length. Tegmentum of intermediate valves much longer than wide, triangular, very reduced relative to the articulamentum.



Explanation of Figures 67 to 72

Figures 67-72. Acanthochitona exquisita (Pilsbry, 1893).

Figure 67. Puertocitos, Baja California, Mexico (GTW) (27 mm).

Figure 68. Lectotype of *Acanthochites exquisitus* Pilsbry, 1893, Las Animas Bay, Baja California, Mexico (ANSP) (29 mm).

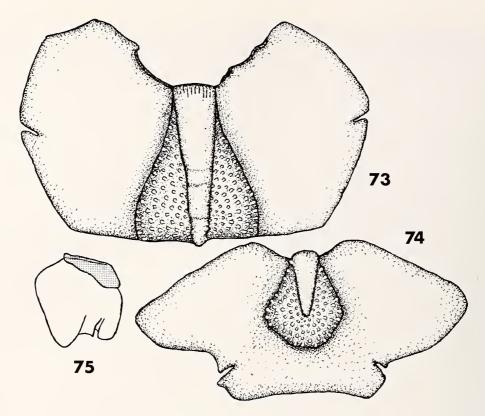
Figure 69. Lectotype of Acanthochites exquisitus variety ampullaceus Pilsbry, 1893, La Paz, Baja California, Mexico (ANSP) (20 mm).

Figures 70, 72. Acanthochitona exquisita (Pilsbry, 1893), Bay of Panama, Panama (GTW).

Figure 70. Dorsal view of pustules (scale = $100 \mu m$).

Figure 71. Oblique view of pustules (scale = $100 \mu m$).

Figure 72. Dorsal view of jugum (scale = $100 \mu m$).



Explanation of Figures 73 to 75

Figures 73–75. Acanthochitona exquisita (Pilsbry, 1893), Puertocitos, Baja California, Mexico (GTW).

Figure 73. Intermediate valve VII (8.2 mm width).

Figure 74. Posterior valve (6.3 mm width).

Figure 75. Posterior valve profile.

Beaks not prominent, posterior border of intermediate valves nearly straight. Jugum smooth, very narrow, sides nearly parallel. Jugal macresthetes arranged in longitudinal rows, each accompanied by 0–3 micresthetes. Latero-pleural areas sculptured with numerous broad, teardrop-shaped pustules. Each pustule bearing one slightly posteriorly acentric macresthete with no micresthetes. Mucro posteriorly acentric, prominent, postmucronal slope slightly concave. Tegmentum uniformly dark greenish-brown.

Apophyses very extensive. Slit formula 5-1-2. Articulamentum white with flushes of green or blue towards beak.

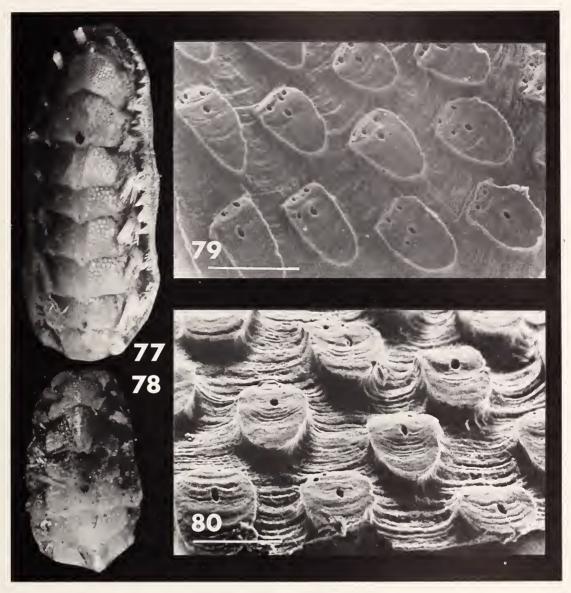
Girdle dorsum densely covered with numerous smooth, straight needlelike spicules. Dorsum colored dark olivegreen. Sutural tufts enormous, consisting of numerous very long, needlelike spicules that may conceal the tegmentum and most of girdle. Tufts and marginal fringe colored bronze, yellow, or dark translucent green.

An exceptional specimen from Las Animas Bay (USNM 58830) has tegmentum and sutural tufts colored goldenorange with white girdle, probably representing an albinistic specimen.



Figure 76

Distribution of Acanthochitona exquisita (Pilsbry, 1893).



Explanation of Figures 77 to 80

Figures 77-80. Americhiton arragonites (Carpenter, 1857). Figure 77. Salinas, Ecuador (GTW) (4 mm).

Figure 78. Lectotype of *Acanthochites arragonites* Carpenter, 1857, Mazatlán, Sinaloa, Mexico (BMNH) (3 mm).

Material examined: MEXICO: BAJA CALIFORNIA: Bahía Carlos (a

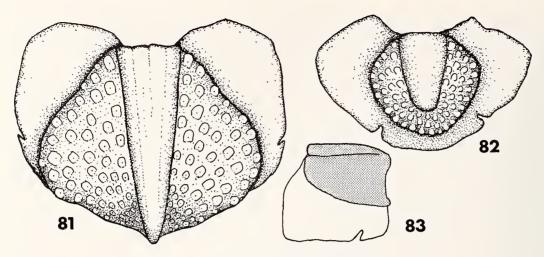
Las Animas (USNM); Bahía de Los Angeles (AMNH, MCZ); Puerto Refugio (USNM); Isla Angel de La Guarda (AMNH); Bahía San Luis Gonzaga (AMNH, DMNH, USNM); Puertocitos (AMNH, DMNH, GTW, MCZ); Agua de Chale (ANSP); BaJa California Sur: Isla Partida (AMNH, USNM); La Paz (ANSP, DMNH, USNM); Bahía Pinchilingue (USNM); Isla San Francisco (USNM); Isla San José; Punta Aqua Verde (both USNM); Isla Danzante; Isla Carmen; Isla Coronados; Bahía de San

Figures 78, 79. Bahía Kino, Sonora, Mexico (GTW) (10 mm) Figure 78. Dorsal view of pustules (scale = $100 \mu m$).

Figure 79. Oblique view of pustules (scale = $100 \mu m$).

Carlos (all AMNH); SONORA: Puerto Libertad; Isla Tiburon (both USNM); Bahía Kino (MCZ). EL SALVADOR: La Libertad (ANSP, MCZ). Costa Rica: Puerto Culebra (ANSP). Panama: Bay of Panama (UMMC).

Remarks: Pilsbry introduced the variety *ampullacea* for specimens possessing wider valves than those of the typical form. An examination of available material clearly shows a continuous range of variation in the width of the tegmentum in specimens from the same locality. LELOUP



Explanation of Figures 81 to 83

Figures 81-83. Americhiton arragonites (Carpenter, 1857), Bahía Kino, Sonora, Mexico (GTW).

Figure 81. Intermediate valve VII (2.4 mm width).

Figure 82. Posterior valve (1.8 mm width).

Figure 83. Posterior valve profile.

(1941) illustrated some interesting examples of malformed specimens.

There is an absence of specimens from Sonora to El Salvador in the collections that I have examined. This striking species is more common than is generally thought and the discontinuity cannot be readily ascribed to a lack of collecting. I cannot detect any difference between the northern and southern specimens and the apparent hiatus cannot be explained at this time.

This is one of the most distinctive species of this family and cannot easily be confused with any other acanthochiton. The nearest relatives of *Acanthochitona exquisita* are *A. rhodea*, *A. hemphilli*, and *A. ferreirai*; all three species are also large chitons with girdles encroaching on the tegmentum. The brick-red tegmentum and minutely spiculose girdle both serve to separate these species from *A. exquisita*. Large specimens of *A. hirudiniformis hirudiniformis* occasionally may approximate this species in the development of the sutural tufts and overall coloration, but *A. exquisita* differs in its greatly reduced tegmentum.

This species is apparently locally common. McLean (1961:453) reported 30 individuals on the underside of a single rock.

As with Acanthochitona rhodeus and A. hemphilli, A. exquisita was described in the July number of The Nautilus, not the Manual of Conchology as is generally believed. The variety ampullaceus does originate from the Manual, however.

Americhiton Watters, gen. nov.

Type species: Acanthochites arragonites Carpenter, 1857, by original designation herein.

Diagnosis: Small chitons, vermiform, tegmentum of intermediate valves pentagonal, each about as wide as long. Tegmentum sculptured with convex, D-shaped pustules, each bearing 1 or 2 macresthetes with micresthetes confined to prepustular slope. Esthete innervations sandwiched between tegmentum and articulamentum, no myostracum palleale apparent. Apophyses moderately extensive. Slit formula 5-1-2+. Dorsal girdle elements mono- or bimorphic; sutural tufts large but composed of relatively few spicules; ventral spicules monomorphic, flattened in cross-section, smooth.

Remarks: This genus superficially resembles some species of Craspedochiton s.l., but the absence of interpustular esthetes, which have been found in all species of Craspedochiton that I have examined, suggests a closer relationship to Acanthochitona. The genus Americhiton contains A. arragonites from the eastern Pacific and the following western Atlantic species: A. andersoni (Watters, 1981), A. balesae (Abbott, 1954), and A. zebra (Lyons, 1988).

This genus differs from Acanthochitona in the form of the pustules and the esthete distributional pattern. It has D-shaped convex pustules rather than oval or teardrop-shaped concave pustules, and micresthetes generally limited to the prepustular slope rather than distributed across the pustule. The four described species are all small, vermiform, and limited to the New World. They form a cohesive group of chitons quite different from other New World species and constitute a separate genus. Vermiform Old World species appear to belong to Acanthochitona, e.g., A. penetrans (Winckworth, 1933) and A. shirleyi (Ashby, 1922). Ferreira (1985) synonymized species of this genus with Choneplax lata, a cryptoplacine; this confusion ap-

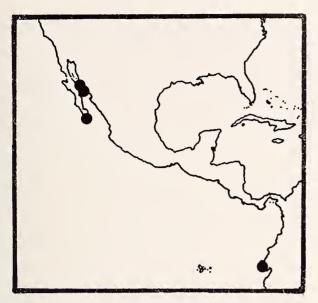


Figure 84

Distribution of Americhiton arragonites (Carpenter, 1857).

parently arose from his misidentification of small adult chitons as juvenile specimens of larger species.

Etymology: A combination of "America" and the standard "-chiton" ending; the known species are confined to the Americas.

Americhiton arragonites (Carpenter, 1857)

(Figures 77-84, 90)

Acanthochites arragonites Carpenter, 1857:190; Carpenter, 1864:650; Carpenter, 1872:136; Pilsbry, 1893b:25, 26; Nierstrasz, 1905:60; Brann, 1966:46; pl. 12, fig. 258; Keen, 1968:433; pl. 59, fig. 82.

Acanthochites arragonitei [sic] Carpenter: CARPENTER, 1866: 211.

Acanthochites arragonite [sic] Carpenter: CARPENTER, 1866: 211

Acanthochitona aragonites [sic] (Carpenter): Dall, 1919:515.

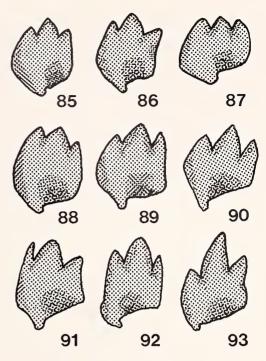
Acanthochiton arragonites (Carpenter): Leloup, 1941:3, 9;

FISCHER, 1978:37.

Acanthochitona arragonites (Carpenter): STEINBECK & RICK-ETTS, 1941:551; CHACE, 1958:331; KEEN, 1958:519; KEEN, 1968:433; pl. 59, fig. 92; THORPE, 1971:866; fig. 10; ABBOTT, 1974:407; SMITH & FERREIRA, 1977:94; KAAS & VAN BELLE, 1980:10; WATTERS, 1981b:175, 176; pl. 2h-j; pl. 4k; Lyons, 1988a:112; SKOGLUND, 1989:87.

"Acanthochitona cf. A. arragonites (Carpenter)": Dushane & Sphon, 1968:244.

Type material: Lectotype, by designation of KEEN (1968: 414), BMNH 1857.6.4.907, a loose, partially disarticulated specimen; paralectotype, four valves of another glued onto a glass strip.



Explanation of Figures 85 to 93

Figures 85–93. Representative denticle caps from the radulae of New World Cryptoplacidae (median to the right; measurements are for widths).

Figure 85. Americhiton balesae (Abbott, 1954), Galeta Point, Canal Zone (east) (RCB). $100~\mu m$.

Figure 86. Paratype of Americhiton andersoni (Watters, 1981), Picquet Rocks, Bimini, Bahamas (DMNH). 100 μ m.

Figure 87. Acanthochitona angelica (Dall, 1919), María Magdelina Id., Tres Marias Ids., Mexico (AMNH). 200 μm .

Figure 88. Acanthochitona avicula (Carpenter, 1864), Agua de Chale, Baja California, Mexico (AMNH). 200 µm.

Figure 89. Acanthochitona imperatrix Watters, 1981, La Paz, Baja California Sur, Mexico (USNM). 100 µm.

Figure 90. Americhiton arragonites (Carpenter, 1857), Bahía Kino, Sonora, Mexico (GTW). 100 μ m.

Figure 91. Choneplax lata (Guilding, 1829), Galeta Point, Canal Zone (east) (RCB). 150 $\mu m.$

Figure 92. Acanthochitona hirudiniformis hirudiniformis (Sowerby I, 1832), Isla Pinzón (Duncan Id.), Galápagos Ids., Ecuador (GTW). 300 μ m.

Figure 93. Acanthochitona exquisita (Pilsbry, 1893), Puertocitos, Baja California, Mexico (GTW). 300 μm.

Type locality: "Mazatlan," (Sinaloa, Mexico).

Description: Largest specimen, 12 mm in length. Tegmentum of intermediate valves longer than wide, pentagonal in outline. Jugum smooth, very wide. Jugal macresthetes arranged in longitudinal rows, each accompanied by 1–7 micresthetes. Latero-pleural coarsely granulose, the

pustules D-shaped. Each pustule bearing one macresthete located acentrically towards beak, with 2-4 micresthetes predominantly confined to premacresthete area. Mucro posteriorly acentric, very prominent, postmucronal slope steep and concave. Tegmentum uniformly china white, green, brown, or variegated with these colors; jugum may differ in color from latero-pleural areas.

Apophyses not extensive. Slit formula 5-1-2. Articulamentum white or green, tinged with rose towards beak.

Dorsum of girdle velvety, covered with minute, finely ribbed, bent monomorphic elements. Dorsum white, mottled with green and brown. Sutural tufts and marginal fringe well-developed, colored translucent white or green. Marginal fringe bimorphic; larger elements finely ribbed; both bent.

Distribution: Intertidally to 20 m from Sonora, Mexico to Salinas, Ecuador.

Material examined: MEXICO: BAJA CALIFORNIA SUR: Cabo San Lucas (USNM); SONORA: Guaymas, N of Bahía San Carlos, Ensenada Lalo (DMNH); Bahía Kino (GTW). ECUADOR: Salinas (GTW).

Remarks: Specimens of this species are rare in collections and are usually misidentified as small examples of *Acanthochitona avicula*. PILSBRY (1893b:26) remarked "it would be difficult to find a shell of such surpassing beauty"; nevertheless he did not illustrate it, and the species remained unfigured until BRANN (1966), 73 years later.

This species is most closely related to Americhiton and acroni and A. zebra, all of which have the pustules of the intermediate valves in a radiating pattern from the jugum; in A. balesae, the pustules parallel the jugum.

ACKNOWLEDGMENTS

The author would like to thank the following people, who graciously loaned me material or assisted while I visited their institutions: J. Rosewater, H. Rehder, M. Harasewych, and P. Greenhall, National Museum of Natural History, Washington, D.C.; W. Clench, R. Turner, and K. Boss, Museum of Comparative Zoology, Cambridge, Massachusetts; W. Emerson, W. Old, and W. Sage, American Museum of Natural History, New York, New York; R. Robertson, G. Davis, and M. Miller, Academy of Natural Sciences, Philadelphia, Pennsylvania; R. T. Abbott and R. Jensen, Delaware Museum of Natural History, Greenville, Delaware; K. Way and S. Morris, British Museum (Natural History), London, England; B. Burkett, University of Miami, Coral Gables, Florida; A. D'Attilio, San Diego Museum of Natural History, California; D. Stansbery and C. Stein, Museum of Zoology, Ohio State University, Columbus, Ohio; A. J. Ferreira, California Academy of Sciences, San Francisco, California; P. Kaas, Rijksmuseum van Natuur-Lijke Historie, Leiden, Netherlands; and C. J. Finlay, Palm Bay, Florida.

This work originally was completed as partial fulfill-

ment of the Master's Thesis at the University of Rhode Island. I would like to thank my committee for their valuable criticisms and guidance: J. Heltsche, K. Hyland, and particularly R. C. Bullock.

Portions of this work were supported by a Sigma Xi Grant-in-Aid of Research and a scholarship from the National Capital Shell Club.

Two reviewers offered valuable suggestions and criticisms; their comments are greatly appreciated.

LITERATURE CITED

ABBOTT, R. T. 1974. American seashells. 2nd ed. Van Nostrand & Reinhold: New York. 663 pp.

ABBOTT, R. T. & S. P. Dance. 1982. Compendium of seashells. E. P. Dutton: New York. x + 414 pp.

ADAMS, A. 1847. Notes on certain molluscous animals. Proc. Zool. Soc. London for 1846:19–26.

ADAMS, H. 1861. Descriptions of some new genera and species of shells from the collection of Hugh Cuming, Esq. Proc. Zool. Soc. London for 1860:383-385.

ADAMS, H. & A. ADAMS. 1858. The genera of Recent Mollusca, 1. Van Voorst: London. 484 pp.

ASHBY, E. 1922. Notes on Australian Polyplacophora, with descriptions of three new species and two new varieties. Trans. Proc. Roy. Soc. S. Australia 46:9-22.

ASHBY, E. 1926. The acanthoid chitons of New Zealand. Proc. Malacol. Soc. London 17:5-35.

BARATTINI, L. P. 1951. Malacologia Uruguaya. Publicaçiones Científicas, Servicio Oceanográfico y de Pesca (6):181–293.

Bergenhayn, J. R. M. 1930. Kurze Bemerkungen zur Kenntnis der Schälenstruktur und Systematik der Loricaten. Kungliga Svenska Vetenskapsakademien Handlingar (3)9(3): 3-54.

Bergenhayn, J. R. M. 1937. Antarktische und Subantarktische Polyplacophora. Sci. Results Norwegian Antarctic Exped. 1927–1928:12 pp.

Bergenhayn, J. R. M. 1955. Die fossilen Schwedischen Loricaten nebst einer vorlaüfigen Revision des Systems der ganzen Klasse Loricata. Lunds Universitets Årsskrift, (n.s.) 2, 51(8) (Kungliga Fysiografiska Sällskapets Handlingar, (n.s.) 66(8)):1-41.

BERRY, S. S. 1922. Fossil chitons of western North America. Proc. Calif. Acad. Sci. 11:399-526.

BIOLLEY, P. 1907. Mollusques de L'Isle des Coco. Museum Nacional de Costa Rica: San José. 30 pp. [not seen].

Boss, K. J., J. Rosewater & F. A. Ruhoff. 1968. The zoological taxa of William Healey Dall. Bull. U.S. Natl. Mus. (287):427 pp.

Brann, D. C. 1966. Illustrations to "Catalogue of the collection of Mazatlán Shells" by P. P. Carpenter. Paleontological Research Inst.: Ithaca. 111 pp.

Bullock, R. C. 1974. Book review: Polyplacophora of the Caribbean region, by P. Kaas. Malacol. Rev. 7:163-164.

BULLOCK, R. C. 1988. The genus *Chiton* in the New World (Polyplacophora: Chitonidae). Veliger 31:141-191.

BURCH, J. Q. 1946. Check list of west North America marine mollusks. Minutes Conch. Club S. Calif. (66):17-19.

Burghardt, G. E. & L. E. Burghardt. 1969. A collector's guide to west coast chitons. San Francisco Aquarium Soc., Spec. Publ. (4):45 pp.

Burrow, E. I. 1815. Elements of conchology. London. xix + 245 pp.

- CARCELLES, A. R. 1950. Catálogo des los moluscos de la Patagonia. Annali Museo de Nahuel Huapí Perito 2:41-100.
- CARCELLES, A. R. 1953. Catálogo de la malacofauna Antarctica Argentina. Annali Museo de Nahuel Huapí Perito 3:155– 250.
- CARCELLES, A. R. & S. I. WILLIAMSON. 1951. Catálogo de los moluscos marinos de la provincia Magellanica. Revista del Instituto Nacional de Investigaçión de las Ciencias Naturales anexo al Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Zoología 2(5):243-250.
- CARPENTER, P. P. 1857. Catalogue of the collection of Mazatlán shells in the British Museum: collected by Frederick Reigen. British Museum: London. i-iv, ix-xvi, 552 pp.
- CARPENTER, P. P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Rept. British Assoc. Adv. Sci. for 1863, 33:517-686 (reprinted 1872, Smithsonian Misc. Coll. 10(252):172 pp.).
- CARPENTER, P. P. 1866. Descriptions of new marine shells from the coast of California, part III. Proc. Calif. Nat. Acad. Sci. 3(1):207–224.
- Castellanos, Z. J. A. de. 1948. Sobre seis especies de Poliplacoforos Argentinos. Notas Zoología, Museo de La Plata 13:191-202.
- CASTELLANOS, Z. J. A. DE. 1951. Poliplacoforos del Museo Argentinos de Ciencias Naturales. Communicaciónes del Instituto Nacional de Investigaçión de las Ciencias Naturales anexo al Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Zoología 1(15):31 pp.
- CASTELLANOS, Z. J. A. DE. 1956. Catálogo de los Poliplacoforos Argentinos y de aguas vecinas al Estrecho de Magellanes. Revista Sección Zoología, Museo de La Plata, (n.s.) 6:465–486.
- CHACE, E. P. 1958. The marine molluscan fauna of Guade-loupe Island, Mexico. Trans. San Diego Soc. Natur. Hist. 12(19):319-332.
- CLENCH, W. J. & R. D. TURNER. 1962. New names introduced by H. A. Pilsbry in the Mollusca and Crustacea. Acad. Natur. Sci. Philadelphia, Spec. Publ. (4):218 pp.
- CLESSIN, S. 1903–1904. Die Familie Chitonidae. Pp. 1–96 [1903]; pp. 97–135 [1904]. *In:* Martini & Chemnitz, Systematisches Conchylien-Cabinet. 2nd ed., 6(4). Hürnberg.
- COAN, E. V. 1968. A biological survey of Bahía de Los Angeles, Gulf of California, Mexico. III. Benthic Mollusca. Trans. San Diego Soc. Natur. Hist. 15(8):109–132.
- COOPER, J. G. 1867. Geographical catalogue of the Mollusca found west of the Rocky Mountains between latitudes 33° and 49° North. California State Geol. Survey, and Towne & Bacon: San Francisco. 40 pp.
- DALL, W. H. 1876. Mollusks. Pp. 42-49. In: J. H. Kidder, Contributions to the natural history of Kerguelen Island, made in connection with the U.S. Transit-of-Venus Expedition, 1874-75, II. Bull. U.S. Natl. Mus. 3.
- Dall, W. H. 1879a. Report on the limpets and chitons of the Alaskan and Arctic regions, with descriptions of genera and species believed to be new. Sci. Results Expl. Alaska, art. 4: 63–126.
- Dall, W. H. 1879b. Report on the limpets and chitons of the Alaskan and Arctic regions, with descriptions of genera and species believed to be new. Proc. U.S. Natl. Mus. 1:281–344.
- Dall, W. H. 1882. On the genera of chitons. Proc. U.S. Natl. Mus. 4:279–291.
- Dall, W. H. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Pe-

- ruvian zoological province. Proc. U.S. Natl. Mus. 37:147–294.
- DALL, W. H. 1919. Descriptions of some new species of chitons from the Pacific coast of America. Proc. U.S. Natl. Mus. 55: 499–516.
- DANCE, S. P. 1973. Sea shells. Bantam Books: New York. 159 pp.
- DUNKER, W. B. 1882. Index molluscorum maris japonici. Cassel. 301 pp.
- DUSHANE, H. 1962. A checklist of mollusks for Puertocitos, Baja California, Mexico. Veliger 5:39-50.
- DUSHANE, H. & G. G. SPHON. 1968. A checklist of intertidal mollusks for Bahía Willard and the southwestern portion of Bahía San Luis Gonzaga State of Baja California, Mexico. Veliger 10:233-246.
- Ferreira, A. J. 1985. Chiton (Mollusca: Polyplacophora) fauna of Barbados, West Indies, with the description of a new species. Bull. Mar. Sci. 36(1):189–219.
- FERREIRA, A. J. 1987. The chiton fauna of Cocos Island, Costa Rica (Mollusca: Polyplacophora) with the description of two new species. Bull. S. Calif. Acad. Sci. 86:41–53.
- FINET, Y. 1985. Preliminary faunal list of the marine mollusks of the Galápagos Islands. Institut Royal des Sciences Naturelles de Belgique, Documents de Travail (20):1–50.
- FISCHER, P.-H. 1978. L'habitat littoral parmi les mollusques polyplacophores. Jour. Conchyl. 115:30-55.
- FREMBLY, J. R. N. 1827. A description of several new species of chitons, found on the coast of Chili, in 1825, with a few remarks on the method of taking and preserving them. Zool. Jour. 3:193–205.
- GOULD, A. A. 1846. On the shells collected by the United States Exploring Expedition. Proc. Boston Soc. Natur. Hist. 2(14): 141–145.
- GRAY, J. E. 1821. A natural arrangement of Mollusca, according to their internal structure. London Medical Repository, Monthly Journal, and Review 15:229–239.
- Gray, J. E. 1843. Catalogue of the species of Mollusca. Pp. 228–265. *In:* E. Dieffenbach, Travels in New Zealand; with contributions to the geography, geology, botany, and natural history of that country, 2.
- GUILDING, L. 1829. Observations on the Chitonidae. Zool. Jour. 5:25–35.
- HADDON, A. C. 1886. Report on the Polyplacophora collected by H.M.S. "Challenger" during the years 1873–1876. Zool. Challenger Exp. 43:47 pp.
- HERRMANNSEN, A. N. 1846–1847. Indicis generum Malacozoorum primordia, 1. T. Fisheri: Cassell. 637 pp.
- HERTLEIN, L. G. 1963. Contributions to the biogeography of Cocos Island, including a bibliography. Proc. Calif. Acad. Sci. (4)37(8):219–289.
- HOUSTON, R. S. 1973. Mollusca. Pp. 132–180. In: R. C. Brusca, Common intertidal invertebrates of the Gulf of California. Univ. Arizona Press: Tucson.
- HOUSTON, R. S. 1980. Mollusca. Pp. 130–204. *In*: R. C. Brusca, Common intertidal invertebrates of the Gulf of California. Univ. Arizona Press: Tucson.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1985. International code of zoological nomenclature. 3rd ed. Univ. California Press: Berkeley. 338 pp.
- IREDALE, T. 1915. Some more notes on Polyplacophora. Proc. Malacol. Soc. London 11:126–129.
- IREDALE, T. & A. F. B. HULL. 1925. A monograph of the Australian loricates. Australian Zool. 4(5): 75–111.
- KAAS, P. 1972. Polyplacophora of the Caribbean region. Studies on the Fauna of Curação 41(137):162 pp.